# BULLETIN of CARNEGIE MUSEUM OF NATURAL HISTORY 

# REEVALUATION OF EARLY MIOCENE NORTH AMERICAN MOROPUS (PERISSODACTYLA, CHALICOTHERIIDAE, SCHIZOTHERIINAE) 

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#### Abstract

The subfamily Schizotheriinae, as represented by the genera Schizotherium, Borissiakia, Moropus, Phyllotillon, and Ancylotherium, is distinguished from the Chalicotheriinae by its more elongated, higher crowned molar teeth and less progressive foot structure. Of these genera, only Moropus ever reached North America, arriving in the medial or late Arikareean. Four late Arikareean/early Hemingfordian species of Moropus are recognized. Moropus distans, the type species, is represented by a few posteranial remains of small size. Based on comparison with other Moropus species, it is closely related to, and may be synonymous with, Moropus oregonensis, a species also from the late Arikareean of Oregon but represented only by dental remains. Moropus elatus and Moropus hollandi of the Great Plains


ABSTRACT
include individuals near the large end of Moropus size range and are more closely related to one another than either is to $M$. distans or $M$. oregonensis. M. elatus is quite well known from numerous individuals and is an important basis for studies of intraspecific variation and interspecific and intergeneric comparisons. $M$. hollandi is unique among Moropus species in having lost the trapezium from the manus. Moropas senex, represented by a single phalanx from Oregon, is considered a nomen dubium. Moropus is known to have ranged from Oregon to Florida in the late Arikareean and also occurs in the Aquitanian of France. Fragmentary, scattered remains are the worst barrier to an understanding of the early evolutionary history of this genus.

## INTRODUCTION

Excavations by Carnegie Museum of Natural History expeditions at the Agate Spring Quarries in Sioux County, northwestern Nebraska, between 1904 and 1908 provided the major stimulus for the first comprehensive review of North American chalicotheres. In 1914, Holland and Peterson published a complete description of material of Moropus elatus collected by the Carnegie Museum of Natural History at Agate and included a comparison with known remains of Moropus hollandi and other species of Moropus. No broad rediscussion of Moropus has appeared since. In 1970, I began a restudy of the Schizotheriinae (Coombs, 1973), with
special emphasis on Hemingfordian and later North American relatives of $M$. elatus. This later material had been only peripherally studied by Holland and Peterson, and much new material had appeared. Some of the results of this study have been published (Coombs, 1974, 1975, 1976), but before a complete reevaluation of the later species will be meaningful, it is necessary to rediscuss the early Miocene North American species of Moropus using newer material and data. Planned functional and zoogeographic considerations of Moropus also necessitate this reevaluation.

## ABBREVIATIONS AND USAGE

The following museum abbreviations are used with specimen numbers:

[^0]A. Dorsal-ventral as applied to the skull, vertebrae, and pelvis;
B. Anterior-posterior as applied to skull (including toothrows), vertebrae, pelvis, scapula, and long bones of fore and hind limbs;
C. Dorsal-volar (=anterior-posterior, dorsal-ventral, dorsalplantar of several other authors) for carpals, metacarpals, tarsals, metatarsals, and phalanges;
D. Radial-ulnar (=medial-lateral) for carpals, metacarpals, and phalanges of the manus;
E. Tibial-fibular (=medial-lateral) for tarsals, metatarsals, and phalanges of the pes; and
F. Labial-lingual in reference to the teeth.

The three phalanges of each digit are named. respectively, proximal, medial, and ungual (the latter is the fissured claw); this designation is to avoid the confusion with digit numbers (I-V), which results when the phalanges are aiso given numbers. Fused proximal and medial phalanges of digit 11 of the manus and occasionally also of digit II of the pes are termed duplexes following the usage of Holland and Peterson (1914).

## STRATIGRAPHIC DISTRIBUTION

Skinner`s report (1968) correlating chalicotheriid occurrences in North America provided an important basis on which the present study could build. Nevertheless, new chalicothere finds, discovery of additional specimens in old collections, further data concerning the location or correlation of old localities, and the greater knowledge acquired through further taxonomic study all make necessary a rediscussion of stratigraphic distribution. A map of the localities discussed is provided in Fig. 1. Localities yielding chalicotheres of medial Hemingfordian or later age and of uncertain age will be discussed in later papers. Although chalicothere remains can give some idea of the correlation of deposits, they are usually too rare and too incomplete to be of much practical value in biostratigraphy.

John Day Formation.—Skinner (1968:12-13) suggested that Moropus distans and M. senex, species established by Marsh from the John Day Basin, could be from the Rattlesnake Formation or Mascall Formation in the region, as well as from the John Day Formation. Some additional data, which suggest that at least some of Marsh’s material is from the John Day Formation, are available.

Specimen labels on Moropus material from the John Day Basin give the following general locality information: 1)YPM 12193a, holotype of Moropus distans-"Bridge Creek beds" (Marsh specimens included in the hypodigm have the same collecting data); 2) YPM 12194, holotype of M. senex-"Dayville?, Oregon"; 3) YPM 10030, holotype of $M$. or-egonensis-"Upper John Day beds, Bridge Creek, Wasco County, Oregon." collected by Condon (additional specimens from the same locality catalogued as YPM 10030a, 10030b); 4) AMNH 7259, referred by Holland and Peterson (1914) to M. or-egonensis-"near Antelope Springs, Oregon." Although none of this data is precise enough to suggest exact locations, at least the "Bridge Creek beds" included important early collecting areas in the John Day Formation. The size and morphology of the specimens is near that hypothesized for early Miocene Moropus immigrants to North America and may suggest a relatively early age for the John Day chalicotheres. However, the designation of "Upper Joha Day beds" for the holotype of $M$. oregonensis signifies no more than that the specimen proba'sly came from the John Day Formation. As Hay (1963), Rensberger (1971, 1973), and Fisher
and Rensberger (1972) have pointed out, the boundaries as designated by Merriam (1901) between members of the formation are not synchronous everywhere in the area. Fisher and Rensberger (1972) recently advocated a four-fold division of the John Day Formation; the divisions between members cross biostratigraphic boundaries, especially the division between the Turtle Cove Member and Kimberly Member. Fisher and Rensberger (1972:9) also pointed out the difficulties of using adherent matrix as a criterion for assigning formerly collected museum specimens to members of the John Day Formation.

Further information concerning distribution of chalicothere remains in the John Day Formation may be forthcoming. In the John Day stratigraphic collection being studied by Rensberger is a small chalicothere phalanx. Rensberger, who intends to describe the occurrence along with the remainder of his perissodactyl collection, stated (personal communication, 1972) that the specimen came from a stratigraphic level, which represents an early or possibly medial Arikareean age. Although some of the earlier collected Moropus material from the John Day Basin may be younger than this, John Day chalicotheres are clearly among the earliest known representatives of Moropus in North America.

Harrison Formation and Upper Harrison Formation (=Marsland Formation sensu McKenna, 1965), Nebraska and Wyoming.-The highest frequency of Moropus specimens, including material of both $M$. elatus and $M$. hollandi, occurs in these two formations. Recently, Robert M. Hunt of the University of Nebraska has restudied the type areas of both formations and traced the contact between them to important fossil localities. One of the most far-reaching results of his study has been the conclusion that the Harrison-Upper Harrison contact lies below the Agate Spring Quarries and that therefore the well-known fossil assemblage from these quarries comes from the Upper Harrison Formation (Hunt, personal communication, 1976). By Hunt’s reinterpretation, the fauna associated with the Harrison Formation is relatively sparsely known, but it does include isolated specimens of chalicotheres probably referable to M. elatus. Chalicotheres from the Agate Spring Quarries are in the present paper attributed to the Upper Harrison Formation, in accordance with Hunt's findings.


Fig. 1.-Map of Arikareean-early Hemingfordian Moropus iocalities discussed in this paper: 1) Caliente Formation, California; 2) Dayville, Oregon (type of "M. senex"); 3) Bridge Creek, near Mitchell, Oregon (types of $M$. distans and $M$. oregonensis); 4) near Antelope Springs, Oregon; 5) Lemhi River Valley, 46 mi southeast of Salmon, Idaho; 6) 7 mi south of Chugwater, Platte Co., Wyoming; 7) Big Muddy Creek, Wyoming; 8) Jay Em, Goshen Co., Wyoming; 9) near Van Tassell, Niobrara Co., Wyoming; 10) western Sioux County along Niobrara River, Nebraska (type of M. hollandi); 11) Agate Spring Quarries and American Museum-Cook Quarry, Sioux Co., Nebraska; 12) Morava Ranch Quarry and surrounding area, Box Butte Co., Nebraska (type of M. elatus?); 13) Buda local fauna, Alachua Co., Florida.

One important problem in discussions of Moropus elatus Marsh has concerned the geographic and stratigraphic position of its type locality in relation to strata exposed in the Agate Spring Quarries. Skinner (1968, Table 1, footnote a) correctly stated that Marsh's type of M. elatus, if from the locality suggested by Holland and Peterson (1914:226). could have come from one of several formations exposed near the mouth of Whistle Creek in Sioux County, Nebraska. However, Matthew (1929:520, footnote 1) had differed from Holland and Peterson's estimation of the locality in concluding that the type of M. elatus was actually found some 18 mi east of Agate, Nebraska, a site well east of that proposed by Holland and Peterson.

Matthew's reason for proposing that the type locality of Moropus elatus was farther east was based on some surface exploration and digging conducted
by Harold J. Cook and communicated by letter to Osborn in 1917 and 1918 and to Matthew in 1927. Cook had concluded that the Agate Quarry vicinity was too distant to have been easily visited from the stage road presumed to have been followed by Marsh's collector Hank Clifford en route between Sidney, Nebraska, and the Red Cloud Agency. Cook had discovered a fossil pocket, which appeared to have been previously worked, relatively close to the stage road and about 18 mi east of Ag ate. Cook collected at this spot some chalicothere material, which he sent to the American Museum for study. Subsequently the specimens were examined by Richard S. Lull and compared with the type material of $M$. elatus at Yale University. Lull concluded (personal communication to Osborn. 1917) that Cook's material was similar in color, preservation, and general appearance to the type.
although no actual break contacts could be found. Unfortunately, I have been unable to locate Cook's specimens for further comparison.

Cook asserted (letter, 1927, quoted in Matthew, 1929:520, footnote 1) that the pocket in which he found the bones "is located in the lower part of the Upper Harrison beds, whereas the Agate Springs Fossil Quarries and the Moropus obtained there are some sixty feet below the top of the Lower Harrison beds." On this basis Matthew (same footnote) stated that the Upper Harrison species M. hollandi was probably synonymous with M. elatus and that the Agate Quarry material should be referable to a different species, M. cooki Barbour. Such a conclusion is not, however, borne out by specimen morphology.

Since Cook's excavation and possible discovery of Clifford's locality, the area between 16 and 20 mi east of Agate along the Niobrara River has been studied by parties of the Frick Laboratory and of the University of Nebraska. The area is complexly channeled and several formations are represented, including the type section of the Runningwater Formation (Cook, 1965). Cook's description of his old diggings stated, "It is really the nearest commanding hill to that old road crossing [Niobrara crossing], so it seems a particularly probable place for him [Clifford] to have found the type specimens [of Moropus elatus] figured and described by Marsh" (letter of 21 November 1917, to Osborn, bracketed material mine). Cook described the matrix as "mostly very hard around the bones, so that collecting is rather slow . . . . As the slope is largely grassed over, it is small wonder that bones at this spot should have missed recent attention by people living around there . . . The color of the matrix varies a good deal locally, and the deposits are quite 'pockety,' due to channel beds, and shifting stream depositions" (H. J. Cook, letter to Osborn, 20 December 1917). These descriptions coincide very closely with the location and lithology of Morava Ranch Quarry, so it seems likely that Cook's locality was at or very near the site of the later quarry, excavated by Ted Galusha in 1940 and by me in 1975. It may also be at or near the original Clifford locality. Moropus remains from Morava Ranch Quarry agree quite well in color (bluish gray) and preservation with the type material of M. elatus. Detailed location of the Morava Ranch Quarry is available in Frick:American Museum records. As mapped in Cook (1965:3), it lies in a Harrison Formation channel, but this assessment may require
reevaluation as study of the area progresses. Morphologic evidence (below) suggests that Agate and Morava Ranch Quarry Moropus are referable to $M$. elatus and that Moropus hollandi is a separate but closely related species.

The Cook Collection at the American Museum of Natural History contains a number of chalicothere remains, primarily teeth and foot elements, from the Agate Quarries and from north and east of Agate. Locality data for some of this material is not sufficient for placement in the Harrison or Upper Harrison Formation. Some material is from the American Museum-Cook Quarry, 2 mi north of the Agate Quarries. This latter locality was discussed in detail by Hunt (1972:35-37) and on the basis of data presented by him is almost certainly the place where American Museum parties collected an excellent skull, AMNH 10,645 , referred to M. elatus. Hunt (personal communication, 1976) now places the American Museum-Cook Quarry in the base of the Upper Harrison Formation.
AMNH 13,765, an upper jaw with $\mathrm{P}^{3}-\mathrm{M}^{3}$ was collected by Olcott in 1907 at the "top [of] Lower Harrison beds, Van Tassel. Wyoming" (specimen field label by Olcott). This specimen yields very little information of specific taxonomic value and is regarded here as Moropus indet. Locality data are not precise enough to be certain that it comes from the Harrison Formation.
A thick section of the Upper Harrison Formation is exposed along the Niobrara River near the Ne -braska-Wyoming state line. It was here that Peterson (1907a, 1909) designated the type section of the Upper Harrison beds. McKenna (1965) considered Peterson's section to be the type section of the Marsland Formation and used "the term Marsland [proposed by Schultz, 1938] as an objective synonym (at the rank of a formation) of the term Upper Harrison beds" ( $1965: 10$, bracketed material mine). In the Upper Harrison faunal list from this area, Peterson (1907a:56) included Moropus ?elatus Marsh, later in the paper (1907a:60) identified as CM 1424, found "near the base of the Upper Harrison beds on the Niobrara in Sioux County, Nebraska, in 1901." Peterson later (1913) made this specimen the type of a new species, M. hollandi. Holland and Peterson (1914:232) further specified the locality as "near Wyoming state line," and the Carnegie Museum catalogue lists further, "near Vantassel." No additional locality data is available. Hunt (personal communication) has found additional Moropus material at Harper Quarry, just above
the Harrison-Upper Harrison contact near the state line.

Additionally, Skinner (1968) mentioned deposits yielding chalicotheres from the Jay Em district, Goshen County, east-central Wyoming, and from 7 mi south of Chugwater, Platte County, southeastern Wyoming. He considered them biostratigraphically equivalent to the Upper Harrison. Further, Riggs collected Moropus material, now at the Field Museum of Natural History, from beds presumably also Upper Harrison equivalents near Jay Em, Wyoming. Where diagnostic specimens are present, the Jay Em and Chugwater chalicotheres seem to be referable to M. hollandi. It is not presently clear to what extent the difference between M. elatus and $M$. hollandi represents an age and/or ecologic distinction between the faunas containing each. Correspondingly, the boundary between Arikareean and Hemingfordian Moropus-containing faunas needs redefinition.

Other Arikareean or early Hemingfordian occur-rences.-Among the specimens collected by Amherst College expeditions of 1907-1908 at Big Muddy Creek, Wyoming, were several chalicothere phalanges. Locality and stratigraphic data with the material are inexact, and the Amherst College catalogue lists Muddy Creek specimens from "Lower Rosebud," "Lower Harrison," and "Upper Harrison" beds. The basis on which these distinctions were made is unclear. Loomis (1909, 1911) published on turtles and camels from Muddy Creek and concluded that they were from "Upper Harrison beds." The type of Testudo brevisterna, he stated, was found near a skeleton of Merychyus minimus and was thought to be "Upper Harrison" on that basis (Loomis, 1911). However, Schultz and Falkenbach (1947) mentioned no representatives of Merychyus from Muddy Creek; they later (1949) listed the Monroe Creek genera Mesoreodon and Merycoides from Muddy Creek. McKenna and Love (1972) reevaluated Oxydactylus gibbi and Protomeryx leonardi, camel species named by Loomis (1911) from Muddy Creek. They referred both species to Miotylopus gibbi (Loomis) and considered it probable that the type specimens came from beneath the Harrison Formation. The Muddy Creek area and Yale and Amherst College collections derived from it need serious restudy. Monroe Creek equivaient beds clearly seem to be represented, but

Upper Harrison equivalents may be present also. The chalicothere phalanges from Muddy Creek are generally similar to and within the size range of Agate Quarry Moropus elatus. They are probably not useful for correlation, but they may be among the earliest known chalicotheriids in North America.

Patton (1967:8) mentioned the presence of a chalicothere in the Buda local fauna, near Newberry, Alachua County, Florida. Skinner (1968) gave a personal communication from Patton, which further identified the remains, whereas Patton and Webb (1970) described it as a "dwarf version of the large chalicothere . . common in western faunas." Patton and Taylor (1971:128) considered the fauna to be earliest Hemingfordian, but Rich and Patton (1975:695) subsequently suggested an Arikareean age. Patton intends to discuss the chalicothere at a future date. It should be noted in regard to the Buda specimen that specimens of small chalicotheres are also known from the John Day Formation in Oregon.

Repenning and Vedder (1961:C-237) reported a chalicotheriid in an Arikareean assemblage from continental deposits in the Caliente Formation of the eastern Caliente Range, California, between their sections 2 and 3 (1961:C-236) and about 3,000 ft above the base of their section. Repenning (personal communication) identified the remains as the proximal one-half of a rather small duplex bone (fused proximal and median phalanges), abraded and badly gnawed by rodents, and a ?chalicothere tooth fragment. Listed in the same fauna (1961:C237) were Oxydactylus brachyodontus $[?=$ Paratylopus cameloides (Wortman)] and Parablastomeryx aff. P. falkenbachi Frick, both restricted elsewhere to the late Arikareean and early Hemingfordian. Geology of this area has recently been detailed by Woodburne (1975).

Skinner (1968:18) mentioned a Moropus phalanx, F:AM 54,900 , collected at the upper end of the Lemhi River Valley, about 46 mi southeast of the town of Salmon, Idaho. The age of the deposits was unknown but considered possibly biostratigraphically equivalent to the Marsland Formation (sensu McKenna, 1965) of the Great Plains. Morphology of the phalanx is not useful taxonomically and does not contribute any further information to a correlation.

## SYSTEMATICS

Class Mammalia<br>Order Perissodactyla<br>Superfamily Chalicotherioidea Gill, 1872<br>Family Chalicotheriidae Gill, 1872<br>Subfamily Schizotheriinae Holland and<br>Peterson, 1914<br>Included Genera

Schizotherium Gervais, 1876; Ancylotherium Gaudry, 1862; Moropus Marsh, 1877; Pliyllotillon Pilgrim, 1910; and Borrissiakia Butler, 1965.

## Known Distribution

Oligocene-Miocene of Eurasia, Miocene of North America, Pleistocene of Africa (usage of Miocene as in Berggren and Van Couvering, 1974).

## Revised Diagnosis

Dental formula I $0 / 1-3$, C $0 / 0$, P $3 / 3$, M $3 / 3$ (anterior dentition not verified in all genera; see Coombs, in press); molar teeth higher crowned than in the Chalicotheriinae, with molars slightly to strongly elongated; protoloph on upper molars complete on unworn teeth; ectoloph on upper molars less strongly slanted than in the Chalicotheriinae (paracone and metacone in labial half of tooth); metastylid always separate from metaconid on lower molars; jaw symphysis typically shorter and diastema relatively longer than in the Chalicotheriinae; Mt III longest metatarsal or Mt III and Mt IV subequal in length; Mc III longest metacarpal; forelimbs versus hindlimbs not so disproportionate in length as in the Chalicotheriinae; proximal phalanges more symmetrical than in the Chalicotheriinae and ungual phalanges less transversely compressed.

## Discussion

The present-day classification of the Chalicotherioidea, which gives the early (primarily Eocene) chalicotheres (=Eomoropidae) equal rank with the later, unmistakably clawed group ( $=$ Chalicotheriidae), originated with Matthew (1929). Within the latter group he distinguished lineages having highcrowned and low-crowned molar teeth, now designated the Schizotheriinae and Chalicotheriinae. He did not, however, name his subgroups or give full family status to the Eomoropidae and Chalicotheriidae. These refinements evolved gradually in the works of later authors.

The accepted subfamilies Chalicotherinae and

Schizotheriinae show better than any other simple taxonomic scheme the evolutionary relationships within the Chalicotheriidae. Particularly, they express the strong morphological and ecological divergence of Chalicotherium and closely related Nestoritherium from the remainder of the Chalicotheriidae. These Chalicotheriinae, while remaining generally conservative in their dental evolution, attained the most specialized limb structure, evident in even the earliest known representatives (Chalicotherium pilgrimi, C. rusingense). Among these unusual limb features are hindlimbs much shorter than forelimbs, loss of trapezium and Mc V , lunate displaced almost entirely onto the magnum, increase in length from Mc II through Mc IV and from Mt II through Mt IV, astragalus articulating with both navicular and cuboid, asymmetrical proximal phalanges with metapodial facet parallel to dorsal surface, and ungual phalanges strongly compressed transversely. Improved knowledge of the Chalicotheriinae is available in Butler (1965) and Schaefer and Zapfe (1971). Schizotheriines remain more conservatively perissodactyl-like in their foot structure but evolve more rapidly in their dentitions by increasing the crown height and length of molars, probably as a selective response to coarser diet. Schizotheriines are often associated with savannah faunas, whereas Chalicotheriinae are more often found with dense woodland assemblages.

Problems exist, however, in making a clear distinction between Chalicotheriinae and Schizotheriinae. Relations of the primitive Oligocene schizotheriine genus Schizotheriulu to the Chalicotheriinae are unclear. Schizotherilum lacks the foot specializations of chalicotheriines, but its molars are not so elongated or high crowned as in other schizotheriines, although several species trend in this direction. More complete knowledge of Schizotherium should settle some of these questions. Another small difficulty arises because certain schizotheriines parallel the Chalicotheriinae in a few aspects of foot structure, although no schizotheriine attains the derived state seen in even the most primitive known chalicotheriines. Several schizotheriine species independently lost the trapezium; some Ancylotherium lost Mc V; the tall astragalus of Borissiakia articulated with the cuboid as well as with the navicular; metatarsal length was gradually reduced in schizotheriine evolution (see Coombs, 1974). On the other hand, a few primitive species of Chali-
cotherium have a metastylid on lower molars, whereas most other chalicotheriines have a small metastylid or none. Parallelism and problematic primitive genera and species are not uncommon phenomena in taxonomic work, however, and in this case provide no special barrier to the acceptance of two chalicotheriid subfamilies.

The Chalicotheriidae made its first known appearance in North America during the Arikareean Land Mammal Age. Only the Schizotheriinae ever appeared in North America. All North American chalicotheriids could have been derived from a single or several Arikareean immigrants belonging to the genus Moropus.

## Genus Moropus Marsh

Moropus Marsh, 1877:249.
Type species.-Moropus distans Marsh, 1877.

## Included Species

Moropus distans; M. oregonensis (Leidy, 1873); M. elatus Marsh, 1877; M. hollandi Peterson, 1913; M. matthewi Holland and Peterson, 1914; M. merriami Holland and Peterson, 1914; and additional presently undescribed species.

## Known Distribution

Arikareean-Barstovian and possibly later faunas of North America (see Skinner, 1968, and Coombs, 1973, for later generically questionable material); Aquitanian-? of Eurasia.

## Diagnosis

1) Dental formula I $0 / 3, \mathrm{C} 0 / 0, \mathrm{P} 3 / 3, \mathrm{M} 3 / 3 ; 2$ ) molars intermediate in proportionate length and crown height between those of Schizotherium and Ancylotherium; 3) absence of a) crochet, b) labial rib on ectoloph between mesostyle and metastyle, and c) accessory cuspules on $\mathrm{M}^{3}$ posterolingual to hypocone; 4) no hypoconulid on $\mathrm{M}_{3}$; 5) frontals and parietals of skull without dorsal expansion; 6) Mc V present; 7) scaphoid never contacting Mc II, even during extreme carpal flexion; 8) volar process on lunate better developed than in Ancylotherium; 9) no dorsal flattening of metacarpals; 10) asymmetrical astragalus; 11) astragalus articulating distally only with the navicular; 12) metatarsals proportionately shorter than in Schizotherium and Borissiakia; 13) Mt III and Mt IV subequal in length; 14) Mt IV having ectocuneiform facet; and 15) proximal and medial phalanges of digit II of the manus fused to form a duplex in all except very young individuals.

## Discussion

Moropus differs from Schizotherium in characters 2, 4, 12, and 15; from Borissiakia in characters 3b, 3c, 11, 12, and 15; from Phyllotillon in characters 3 a and 3 b (but a crochet and posterior ectoloph rib are present only rarely in Phyllotillon); and from Ancylotherium in characters 1 (incisors only), 2, 3a, 3b, 6, 7, 8, 9, 13, and 14. Moropus also differs from Borissiakia, Ancylotherium, and Schizotherium turgaicum in the retention of a trapezium in the manus in all species except Moropus loollandi; this bone was lost independently in several schizotheriine lineages. Moropus, like Ancylotherium, has a tendency to fuse the proximal and medial phalanges of digit II of the pes to form a smaller, more symmetrical duplex than that belonging to the manus. The species included in each of the Old World genera discussed above follows the treatment by Coombs (1974).

Two new schizotheriine genera have recently been named-Huanghotherium Tung et al. (1975) and Gansuodon Wu and Chen (1976). Both genera are based on upper molars and differ from Moropus in the following characters: larger size; greater crown height; smaller hypocone; more prominent, ridge-like cingulum lingual to the protocone. Gansuodon has a large crochet on $\mathrm{M}^{3}$, and Huanghotherium has a trace of one on $\mathrm{M}^{2}$. All of the preceding differences from Moropus are shared similarities among Gansuodon, Huanghotherium, and Ancylotherium. Ancylotherium pentelicum, as figured by Thenius (1953), is almost as large as the type of Gansuodon and resembles it closely. The large $\mathrm{M}^{3}$ of Gansuodon compared to $\mathrm{M}^{2}$ is probably not a valid difference from Ancylotherium, for $\mathrm{M}^{2}$ and $\mathrm{M}^{3}$ of the type of Gansuodon may not be the same individual. Huanghotherium was distinguished especially by its tall ectoloph, whose height on $\mathrm{M}^{3}$ exceeds the width of the tooth. Ancylotherium also has very high-crowned molars, but possibly not so tall as in Huanghotherium; further comparison is necessary. Wide intraspecific ranges of variation are common in schizotheriines, and the Chinese material may in future best be viewed as species within Ancylotherium. It is not clear how Gansuodon and Huanghotherium might be related to probable Ancylotherium postcranials from China already figured by Bohlin (1936; an astragalus) and Colbert (1934, Figs. 13a, d, f; an Mt II and phalanges).

North American schizotheriines from the Arika-


Fig. 2.-Mounted skeleton of Moropus elatas, AMNH 14,375, as reconstructed by Osborn (1919). Courtesy of the American Museum of Natural History.
reean onward form a distinct radiation, probably separate from Old World forms. A European Aquitanian representative of Moropus is also recognized (Moropus sp., Coombs, 1974). Both Schizotherium and Borissiakia are easily distinguished from Moropus, but there are problems in distinguishing Old World representatives of Moropus from Phyllotillon (known from limited material from the Burdigalian of Baluchistan and possibly later from Europe) and from Ancylotherium (Metaschizotherium).

## Moropus elatus Marsh

Moropus elatus Marsh, 1877:250.
Moropus cooki Barbour, 1908:215.
Moropus petersoni Holland, 1908:810.
Moropus parviss Barbour, 1909:222.
Moropus elatus: Peterson, 1907b:733; Holland and Peterson, 1914:222.
Moropus petersoni: Holland and Peterson, 1914:226.
Moropus cooki: Osborn, 1917:131.

Moropus cookei: Osborn, 1919:251, Fig. I.
Moropus cooki: Matthew, 1929:520; von Koenigswald, 1932:22.
Moropus elatus: von Koenigswald, 1932:22.
Moropus elatus, M. petersoni, M. parvus, M. cooki: Colbert, 1935: 13; Belyaeva, 1954:49.
Moropus elatus: Coombs, 1974:275; Coombs, 1975:55.

## Lectotype

Mt II of YPM 13.081 (Fig. 18), collected by Hank Clifford in Nebraska, probably near the Niobrara River (see discussion of locality above), ?Harrison Formation, ?late Arikareean.

## Paralectotypes

YPM 24.631a-d, part of duplex of digit II manus, proximal phalanx, tuber of calcaneum, and proximal end of Mt III (Fig. 19). The paralectotypes were figured as part of the type by Holland and Peterson (1914:223-224).

## Hypodigm

YPM 24,632, cuneiform, patella, and distal end of Mc II (figured as part of the type collection by Holland and Peterson but not mentioned by Marsh. 1877); a large quantity of material, including complete skeletons, from the Agate Spring Quarries, Sioux County, Nebraska, in the Carnegie Museum of Natural History, American Museum of Natural History, University of Nebraska State Museum, and other museums; extensive dental and postcranial material (but no complete skeletons) from Morava Ranch Quarry, 18 mi east of Agate, Box Butte County, Nebraska, in the Frick Collection of the American Museum and the Pratt Museum, Amherst College; and additional fragmentary specimens from various localities in northern Sioux County, Nebraska. All referred specimens are from the Harrison Formation or Upper Harrison Formation (see above).

## Diagnosis

1) Chalicotheres at the middle to large end of Moropus size range; 2) upper molars more proportionately elongate than in $M$. oregonensis; 3) labial metaloph origin on unworn $\mathrm{M}^{3}$ very near mesostyle; 4) no lingual cingula on lower molars; 5) trapezium present and well developed; 6) calcaneum with strong extension of narrow ectal facet onto tuber calcis; 7) navicular facet on tibial surface of cuboid without any proximal extension; 8) Mt II with ectocuneiform facet having primarily fibular orientation and an oblique tibial ridge present on the proximal part of the shaft; and 9) proximal and medial phalanges of digit II of the pes only occasionally fused (approximately $10 \%$ of cases).

## Discussion

Of the Moropus species discussed in this paper, Moropus elatus differs from M. distans in characters 1, 7, and probably 9 , from $M$. oregonensis in characters 1 and 2 , and from $M$. hollandi in character 5. Further, M. elatus has, on average, proportionately longer metatarsals than are known for M. hollandi (Table 6). Most of the other diagnostic features mentioned differentiate $M$. elatus from more advanced Moropus species like M. merriami.
Reasons for synonymizing Moropus petersoni Holland, 1908 (including its junior synonym M. parvus Barbour, 1909) with M. elatus were detailed by Coombs (1975). Individuals previously referred to $M$. petersoni are probably females of $M$. elatus.

Morphologic comparisons between the type of $M$. elatus and Agate material (below) provide evidence that Moropus cooki Barbour, 1908, is also a junior synonym of M. elatus.

I have not been able to locate the large scapula (CM 1776) described by Holland and Peterson (1914:230, 332, Fig. 77) as Moropus (?) maximus. This specimen, from the Agate Spring Quarries, is as figured different from all known scapulae of Moropus, despite the large amount of material and variation known. It is here thought to be either an aberrant specimen of M. elatus or does not belong to a chalicothere. M. (?) maximus must be considered a nomen dubium.

Moropus elatus is the most completely known of all chalicothere species. Agate material collected by the American Museum of Natural History after Holland and Peterson's (1914) monograph, as well as more recently collected specimens from other localities, provide additional information concerning intraspecific variation and other aspects of anatomy. For example, an M. elatus edentulous premaxilla, AMNH 11,321, verifies the ruminant-like vegetation cropping mechanism in this species (Coombs, 1978). Such new data are discussed in the present paper with a brief update of morphology already detailed by Holland and Peterson. This review will be especially useful for comparison with other Moropus species. No attempt at muscular reconstruction or detailed functional analysis is made here; these topics are reserved for a separate paper.

## Description and Comments <br> Dentition

Interpreting specific taxonomic relationship and phylogeny on the basis of dentitions is very difficult within the genus Moropus. This difficulty is unfortunate, because in most cases teeth are better represented in the fossil record than limb elements. Teeth show a great amount of variation in morphology and relative proportions within a single population, in many cases combined with the lack of substantive changes in the teeth between populations, even over a long period of time. Yet changes in the limbs of the same animals have been much greater. It is often impossible to identify an isolated tooth or even several associated teeth below the generic level. All things considered, however, it does appear that a few regular changes in dentition occurred as North American chalicotheres evolved. Some of these changes are in pro-


Fig. 3.-Top: right lateral view of skull of AMNH 11,322. Bottom: lateral view of left mandibular ramus of AMNH 14,427 (coronoid process broken). Both are Moropus elatus from the Agate Spring Quarries, Sioux Co., Nebraska.
portions, others in morphology, often in one part of the toothrow but not in another. Particularly important may be subtle changes in tooth wear (that is, which areas of a tooth are worn first and along what plane). At the same time, tooth wear is often a complicating factor because dentitions that would be similar at the same stage of wear may appear quite different at other stages of wear. For the most part treatment of North American chalicothere dentitions has been inadequate, even when specimens were well known (see Holland and Peterson, 1914:245-250), but several European authors (Borissiak, 1946; Butler, 1965; and others) have given good accounts of variation among teeth of a single species. Possibly the lack of early treatment of dentitions of North American forms was a result of the problems created by intraspecific variation. The ter-
minology used in this section is diagrammed in Fig. 4; upper and lower teeth of M. elatus are shown in Fig. 3 and 5.

## Upper Molars

$M^{3}$.-This tooth is the least worn of the molars in any given toothrow and is easily recognized by the shape of its posterior part. It is approximately the same size as $\mathrm{M}^{2}$, sometimes slightly longer or shorter; $\mathrm{M}^{2}$ is in some cases relatively shortened because of wear. Both teeth are much larger than $\mathrm{M}^{1}$ (see Table 1). In the progression from $\mathrm{M}^{1}$ to $\mathrm{M}^{3}$ the anterior V of the W -shaped ectoloph becomes progressively longer compared to the posterior V . The change in proportions is particularly visible between $\mathrm{M}^{2}$ and $\mathrm{M}^{3}$, for in the latter the ectoloph posterior to the mesostyle is not V -shaped but curves


Fig. 4.-Diagrammatic upper molar, upper premolar, and lower molar of Moropus elatus giving dental terminology used in the text.

Table 1.-Lengths ${ }^{\mathrm{a}}$ and widths ${ }^{\mathrm{b}}$ (in mm) of upper cheek teeth of Moropus elatus. M. hollandi, and M. oregonensis.

| Measurements | $\begin{gathered} C M \\ 2103(\mathrm{R})^{\mathrm{c}} \end{gathered}$ | $\begin{gathered} \text { AM } \\ 9923(\mathrm{~L})^{\mathrm{e}} \end{gathered}$ | $\begin{gathered} \text { AMNH } \\ 11,322(\mathrm{R})^{\mathrm{c}} \end{gathered}$ | $\begin{gathered} \text { AMNH } \\ 14,427(\mathrm{R})^{\mathrm{c}} \end{gathered}$ | $\begin{gathered} \text { FMNH } \\ \text { P12094(L) } \end{gathered}$ | $\begin{gathered} \text { YPM } \\ 10.030 \mathrm{a}, \mathrm{~b}^{\mathrm{e}} \end{gathered}$ | $\begin{gathered} \text { YPM } \\ 10,030^{e} \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Labial length $\mathrm{P}^{2}$ | 21.3 | 21.9 | 20.1 | 20.5 | 18.8 |  |  |
| Width $\mathrm{P}^{2}$ | 21.0 | 20.6 | 20.3 | 16.2 | 16.0 |  |  |
| Labial length $\mathrm{P}^{3}$ | 23.1 | 23.2 | 23.2 | 21.1 | 19.4 | 17.4 |  |
| Lingual length $\mathrm{P}^{3}$ | 21.8 | 21.7 | 21.4 | 18.0 | 18.8 | 15.3 |  |
| Width $\mathrm{P}^{3}$ | 28.3 | 29.1 | 26.9 | 26.0 | 24.4 | 20.3 |  |
| Labial length $P^{4}$ | 26.0 | 25.8 | 23.2 | 25.3 | 22.5 | 19.1 | 18.2 |
| Lingual length ${ }^{4}$ | 24.0 | 24.2 | 22.3 | 22.2 | 20.3 | 16.5 | 17.7 |
| Width $\mathrm{P}^{4}$ | 32.6 | 32.1 | 29.9 | 29.8 | 26.6 | 23.1 | 23.5 |
| Labial length $\mathrm{M}^{1}$ | 41.2 | 35.8 | 35.4 | 37.4 | 35.7 | 25.9 |  |
| Width $\mathrm{M}^{1}$ | 35.2 | 37.6 | 35.9 | 32.9 | 31.7 | 21.4 |  |
| Labial length $\mathrm{M}^{2}$ | 55.9 | 45.7 | 53.0 | 55.3 | 49.6 | 36.5 |  |
| Width $\mathrm{M}^{2}$ | 42.9 | 44.7 | 42.0 | 40.6 | 40.8 | 26.2 |  |
| Labial length $\mathrm{M}^{3}$ | 59.8 | 54.0 | 51.6 | 54.4 | 48.3 | 36.5 |  |
| Width M ${ }^{3}$ | 48.6 | 51.0 | 42.6 | 44.1 | 43.2 | 33.8 |  |
| Length premolar row | 68.5 | 69.3 | 62.7 | 62.4 | 58.1 |  |  |
| Length molar row | 144.3 | 131.5 | 128.3 | 136.2 | 130.1 |  |  |
| Length premolar row/length molar row | 0.47 | 0.53 | 0.49 | 0.46 | 0.45 |  |  |

${ }^{\text {a }}$ Lengths are maximum anterior to posterior dimensions.
${ }^{\mathrm{b}}$ Widths are maximum labial to lingual dimensions, including mesostyle on molars.
${ }^{\text {c }}$ M. elatus from the Agate Spring Quarries and Morava Ranch Quarry (AM 9923).
${ }^{1}$ M. hollandi from near Jay Em, Wyoming.
${ }^{\mathrm{e}} \mathrm{M}$. oregonensis: YPM $10,030 \mathrm{a}=$ left $\mathrm{P}^{3}-\mathrm{P}^{4}$, right $\mathrm{M}^{3} ; \mathrm{YPM} 10,030 \mathrm{~b}=$ left $\mathrm{M}^{1}-\mathrm{M}^{2} ;$ YPM $10,030=$ holotype right $\mathrm{P}^{4}$.


Fig. 5.-Occlusal views of cheek teeth of M. elatus: A) left $P^{2}-M^{3}$ of AMNH 11,322; B) left $P^{2}$ of AM 9564; C) left $P^{2}$ of AM 9922: D) left $P_{2}-M_{3}$ of AMNH 14,427 . A and D from Agate Spring Quarries. Sioux Co., Nebraska. B and C from Morava Ranch Quarry, Box Butte Co.. Nebraska.
posterolingually. The ectoloph of $\mathrm{M}^{3}$ is never worn posterior to the metacone. Correlated with the shortening of the posterior ectoloph, $\mathrm{M}^{3}$ is transversely narrow in its posterior part. All of these features are common to other schizotheriine chalicotheres.

On $\mathbf{M}^{3}$ both parastyle and mesostyle are very strongly developed, whereas the metastyle is comparatively weak. The paracone is usually taller than, and labial to, the metaeone. On many specimens a weak labial rib passes from the base of the ectoloph to the tip of the paracone; there is in no case such a rib passing to the metacone. Development of the protoloph varies among specimens, and its structure is rapidly obscured by wear. In the least worn specimens a protoconule is developed on the protoloph just lingual to the paracone. In most unworn specimens the protoloph is continuous all the way to the protocone but somewhat depressed lingual to the protoconule. In others, slightly more worn, the protoloph is incomplete and there is no connection between protocone and protoconule. Where the protoloph is complete, it curves posterolingually from the protoconule to join the protocone's anterior margin. The protocone is a broad-based, conical cusp with a blunt-pointed tip, which lies barely in the anterior half of the tooth, posterior to the paracone and protoconule. The tip of the protocone is worn only after the lingual surface of the ectoloph is well worn and in the majority of specimens is untouched. Even where the protocone is not still connected to the protoloph, a weak ridge passes anteriorly from its tip.

The anatomy of the metaloph of $\mathrm{M}^{3}$ is fairly uniform, the primary differences resulting from varying degrees of wear. No metaconule is developed in any of the specimens, and the hypocone forms the lingual end of the metaloph, its tip intimately connected to and about the same height as the crest. In a slightly worn specimen the labial origin of the metaloph from the ectoloph is close to the mesostyle (less than 10 mm ). In an older individual, attrition has worn the mesostyle to increase the apparent angle of the fold and has moved the apparent metaloph origin posteriorly so that there is a greater distance between metaloph origin and mesostyle. In the most worn specimens, the original tip of the metacone has been worn off and the apparent metacone is positioned posterior to the original one. This change is because of the attrition of the ectoloph anterior to the metacone but not posterior to it; the ectoloph crest then passes directly posteriorly or
even posterolabially rather than posterolingually from the repositioned metacone.

Bordered by the lophs and cusps of $\mathrm{M}^{3}$ are three valleys, two of which increase in size somewhat during wear. The largest of these is the central valley, lingual to the ectoloph between paracone and metacone, anterior to the metaloph and skirting the posterior base of the protocone. This furrow is open lingually between protocone and metaloph, where it forms a notch in the tooth's lingual outline: in worn specimens there may also be an anterior opening across the worn-down protoloph. Between the protoloph and anterior cingulum is a shallower valley. A third small valley, or postfossette, which decreases in size as wear progresses. is bordered by metaloph and ectoloph between hypocone and metastyle. No crochet, as described by Butler (1965:178) for Chalicotherium rusingense, is present in any specimen, although there is sometimes the hint of a very small crista.

Development of cingula varies, but in each specimen a very weak labial cingulum is present. The anterior cingulum is strong and forms a border for the anterior valley, curving posterolingually to skirt the protocone. Near the protocone it is variable. It may be notched anterior to the protocone to create an anterolingual exit for the central valley where the protoloph is worn down or very low; it may thicken and almost merge with the lingual wall of the protocone, sending off a branch to merge with the protoloph or with the small anterior ridge from the protocone tip; or it may retain its ridge-like cingulum character as it skirts the protocone lingually. In all cases it has some (though variable) ridge-like character along the posterolingual part of the protocone; it may then continue weakly to merge with the hypocone or disappear at the large lingual exit of the central valley [it is never so thickened as in Ancylotherium (Ancylotheriam) pentelicum]. A posterior moderate to well-developed cingulum connects hypocone and metastyle and partially or completely closes off the posterior opening of the postfossette [similar to Ancylotherium (Metaschizotherium) fraasi but not as high as in $A$. (A.) pentelicum].

In those specimens where roots are visible there are three present-two small labial roots and a large anteroposteriorly elongated lingual one. The lingual root sends a connecting crest to the small posterolabial root.
$M^{2}$ and $M^{1}$.—Both these teeth are similar morphologically to $\mathrm{M}^{3}$. In most specimens they are too
worn to give good evidence of structural details, but occasionally (CM 1707A, see Holland and Peterson, 1914:pl. 51) an unworn $\mathrm{M}^{1}$ is preserved in association with a deciduous dentition. Where $\mathrm{M}^{1}$ is unworn it appears larger than it does in a mature toothrow between $\mathrm{P}^{4}$ and $\mathrm{M}^{2}$, where anterior and posterior margins of the tooth have been removed by wear. Prior to wear it is clear that a protoconule and complete protoloph are present, although these are quickly worn away, but the protoloph does not necessarily continue directly onto the protocone.
Heavier wear on $\mathrm{M}^{1}$ and $\mathrm{M}^{2}$ reduces the sharpness of the cusps and increases the relative size of the parastyle in comparison to that of $\mathrm{M}^{3}$. Because of wear on the ectoloph posterior to the metacone on these teeth, the size of the postfossette increases rather than decreases with tooth use. There is a slight notch on the metaloph between metacone and hypocone, and the hypocone is taller relative to the metaloph than on $\mathrm{M}^{3}$. Cingula vary in much the same way as on $\mathrm{M}^{3}$, and root development is also similar. On both $\mathrm{M}^{1}$ and $\mathrm{M}^{2}$ there is a labial ectoloph rib opposite the paracone but none opposite the metacone.

## Upper Premolars

$\mathrm{P}^{2}$ is worn very early in the life of the animal, and its unworn structure is therefore difficult to determine. Holland and Peterson (1914:245) described this tooth in fairly great detail, but their terminology is difficult to understand; the terms here follow those of Butler (1965: 183) for Chalicotherium rusingense (see Fig. 5). In the least worn specimens (for example F:AM 54,449, AM 9,922-Fig. 5C) the ectoloph is nearly straight (not W-shaped). The paracone is in line with the metacone, and there is a very low parastyle. Lingual to the paracone and connected to it by a short crest is a cuspule, probably the protoconule, which is not visible in more worn specimens, though traces of it remain. The single lingual cusp, or protocone, is close to the posterior border of the tooth. Because of its location and because it is connected by a strong crest (metaloph?) to the ectoloph posterior to the paracone, it looks more like a hypocone than a protocone. Labially the cingulum is very weak, but between the parastyle and protocone a prominent cingulum is present on the anterior and lingual edges of the tooth. A small posterior cingulum closes posteriorly the valley between protocone and metacone. The most obvious variation among $\mathrm{P}^{2}$ specimens of this species is the occasional in-
creased development of the protoloph lingual to the protoconule and consequent broadening of the anterior part of the tooth (particularly well shown by CM 2103, the Agate Quarry specimen figured by Holland and Peterson, 1914:pl. 49). In this specimen the protoloph is in some places as tall as the protocone but is separated from the protocone by a deep, broad valley. At its lower, lingual end the protoloph merges with the cingulum, which skirts the protocone lingually.
$P^{3}$ and $P^{4}$ are very similar to one another, but $P^{4}$ is larger and less worn. Its ectoloph has a rudimentary W-shape, formed by differences in height of the various points rather than by changes in curvature or slant of the labial wall, which is still quite straight and flat. The paracone is slightly taller than the metacone, and a medium-sized parastyle is developed. Most of the early wear on the tooth is on the lingual side of the ectoloph but does not obscure relations with the lingual side of the tooth. The protocone, the only lingual cusp, is large and crescentshaped and is the last part of the tooth to be worn. It is connected to the ectoloph by two crests, of which the protoloph is taller in some specimens, the metaloph in others. Both lophs are curved and merge into ectoloph and protocone at either end. Enclosed by ectoloph, protoloph, metaloph, and protocone is a deep central valley. Forster-Cooper (1920) noted a weaker metaloph than protoloph on $\mathrm{P}^{3}$ and $\mathrm{P}^{4}$ of Phyllotillon and used this character to differentiate Phyllotillon from Chalicotherium. Variation of this character within Moropus elatus suggests that such a distinction between Phyllotillon and Moropus does not apply.

As in $\mathrm{P}^{2}$, the cingulum is the most variable feature of $\mathrm{P}^{4}$, although in all specimens the labial cingulum is extremely weak. In CM 2103 the lingual cingulum is very strong and the tooth is therefore anteroposteriorly expanded in its lingual part. The anterolingual cingulum is here taller than the posterolingual one. Lingual to the protocone the cingulum loses its ridge-like nature at two points where it nearly merges with the lingual wall of the protocone. Between these points it is separated from the protocone by a small pit. In other specimens (for example, AMNH 11,322, Fig. 5) the cingula are in general much weaker, and in others the posterior cingulum is more strongly developed than the anterior. The lingual cingulum may also remain completely distinct from the protocone.

The smaller $\mathrm{P}^{3}$ has a less W-shaped ectoloph, a weaker parastyle, and a consistently weaker ante-
rior than posterior cingulum. Variations among specimens of $\mathrm{P}^{3}$ seem generally linked in the same individual to those of $\mathrm{P}^{2}$ and $\mathrm{P}^{4}$.

## Lower Molars

Lower teeth were given less attention by Holland and Peterson (1914) than upper teeth, but at the same time these teeth provide fewer features of taxonomic value. $\mathrm{M}_{3}$, the least worn lower molar, is approximately the same size as (slightly larger than) $\mathrm{M}_{2}$; both are larger than $\mathrm{M}_{1}$. The trigonid is shorter but not narrower than the talonid; each consists of a V -shaped crescent of straight to slightly curved lophids. Trigonid and talonid join at the metaconid-metastylid. The metaconid, the tallest point on the trigonid, is sloped gradually anteriorly so that its base partly closes the lingual opening of the trigonid basin. In an unworn specimen, the protoconid, slightly anterior to the metaconid, is nearly as tall as the metaconid, but in a worn specimen it is considerably lower. The lowest cuspid of the tooth, the paraconid, does not rise above the level of the paralophid; usually the paralophid is the most curved of the four lophids.

On the talonid, the highest point is the metastylid, which in unworn specimens is completely separated from the metaconid at its tip. In more worn teeth the two cuspids are more continuous but still can be distinguished by the grooves between them on both labial and lingual sides. Of approximately equal height but lower than the metastylid are the hypoconid and entoconid, the former slightly anterior to the latter but both well posterior to the metastylid.

The labial part of $\mathrm{M}_{3}$ is more rapidly worn down than the lingual part. Protoconid and hypoconid are worn by the ectoloph of the corresponding upper tooth near parastyle and mesostyle respectively and are eventually abraded to below the level of the lingual cuspids, even the paraconid. Trigonid and talonid basins gradually disappear. As wear progresses the lingual cuspids also become more worn, particularly the metaconid and metastylid, which cut across the lingual end of the protoloph of the upper molar. Finally the entire crown is worn flat.

Cingula on $\mathrm{M}_{3}$ and the other lower molars vary among individuals. They are in all specimens strongest posteriorly, anterolabially, and on the labial side between the bases of protoconid and hypoconid. In many of the specimens no further cingula are visible, but in some the cingulum forms a well-defined ridge all around the labial base of the
tooth. In general, the Morava Ranch Quarry specimens seem to have slightly greater cingulum development than those from the Agate Quarries. On all specimens there is practically no development of a lingual cingulum except at the base of the paraconid, where a weak one may be visible.

Where known in an unworn condition, $\mathrm{M}_{1}$ and $M_{2}$ are very similar to $M_{3}$, but metaconid and metastylid are less deeply separated.

## Lower Premolars

$P_{4}$ is very similar to the molars but differs in several ways. Most importantly, the talonid is reduced in length and height so that it is about the same length as the trigonid; its posterior part is particularly shortened so that the entoconid lies directly lingual to the hypoconid. Both of these cuspids are lower compared to metaconid-metastylid than are their counterparts on the molar teeth. Metaconid and metastylid are barely distinct at their tips and rapidly become confluent during wear. On the trigonid the paraconid is so low or so rapidly worn away that it is not visible. On the labial surface of the tooth the groove between trigonid and talonid slants strongly posteriorly toward its base, thus showing an increase in slant over that in $M_{1}$, which in turn has more slant than on $\mathrm{M}_{2}$ or $\mathrm{M}_{3}$. There is a strong ridge-like cingulum all along the labial base of the talonid, ascending at its anterior end opposite the base of the protoconid.
$\mathrm{P}_{3}$ continues the trend away from molar morphology begun by $\mathrm{P}_{4}$. Here the talonid is shorter than the trigonid as well as lower in height, but it exceeds the trigonid in transverse width. The talonid has only a very small basin which is lost very early during wear to form an oblique flat wear surface. Both posterior cuspids, particuarly the entoconid, are very low and are transversely aligned. The trigonid, in contrast to that of $\mathrm{P}_{4}$, has a welldeveloped paraconid that is approximately as tall as the protoconid and is not rapidly worn away. No separate metastylid is developed. The groove between trigonid and talonid is oblique but shallow, and there is a well-defined cingulum along the labial base of the talonid.
On $P_{2}$ only the protoconid forms a well-developed cuspid, and the talonid is rudimentary. Neither trigonid nor talonid basin remains, for all cuspids are in a straight antero-posterior line. Anterior to the protoconid, at the anterior edge of the tooth, is a distinct but small paraconid. Posterior to the protoconid, at the end of a crest, is the low, indistinct


Fig. 6.-(A and B) Ventral views (anterior at top) of atlases of A) M. elatus, AMNH 14.378, and B) M. hollandi, FMNH P13000. (C and D) Occlusal views of deciduous teeth of M. elatus: C) right $\mathrm{dp}_{2}$-dp of AMNH 86,099 and D) right $\mathrm{dp}^{2}-\mathrm{dp}^{4}$ of AMNH 94,232. A. C, and D from Agate Spring Quarries, Sioux Co., Nebraska; B from vicinity of Jay Em, Goshen Co., Wyoming.
hypoconid. On this tooth there is a weak lingual cingulum opposite trigonid and talonid, and on this cingulum there may be occasional traces of a metaconid and/or entoconid. Compared to the trigonid, the talonid is very short. As Holland and Peterson (1914:243) mentioned, the border of the mandible descends sharply anterior to $\mathrm{P}_{2}$, and there is a long diastema between this tooth and the lower incisors.

## Incisors

Of the anterior teeth, only the three lower incisors are present. Their morphology has been discussed in association with an edentulous premaxilla, AMNH 11,321, from the Agate Quarries (Coombs, 1978). Moropus elatus had a cropping mechanism very similar to that of modern cervids and bovids, except that no lower canine was present. There is some evidence (AMNH 11,322 ) that in aberrant cases a procumbent lower canine or deciduous incisors might have been retained in line with the incisor row.

## Deciduous Teeth

Upper teeth of $M$. elatus juveniles are known from at least five specimens (CM 1707A, CM 1743. CM 1747, CM 1738, AMNH 94,232). Both dp ${ }^{3}$ and $\mathrm{dp}^{4}$ strongly resemble the permanent molars but are smaller and more symmetrical and quadrate than $\mathrm{M}^{1}$; the size difference between $\mathrm{dp}^{4}$ and $\mathrm{M}^{1}$ is greater than that between $\mathrm{dp}^{3}$ and $\mathrm{dp}^{4}$. Because of wear on $\mathrm{dp}^{3}$, the protoconule is not visible and the protoloph is incomplete in all known specimens. On $\mathrm{dp}^{4}$ there is, in the least worn specimens, a visible protoconule and a very low (already almost worn away) continuation of the protoloph to the protocone. A tiny anterolingual cuspule is present on the protocone of $\mathrm{dp}^{4}$ in some cases (CM 1743). Wear on the metaloph causes the hypocone to be taller than the rest of the loph. On all specimens of $\mathrm{dp}^{3}$ and $\mathrm{dp}^{4}$, the labial cingulum is absent.
The elongated, subtriangular $\mathrm{dp}^{2}$ resembles the permanent $\mathrm{P}^{2}$ more than it does the other deciduous teeth. As in $\mathrm{P}^{2}, \mathrm{dp}^{2}$ is broadest in its posterior part, due here to strong development of the hypocone, an isolated conical cusp; any metaloph has been rapidly worn away by wear cutting down the lingual face of the ectoloph. The ectoloph has the parastyle in a straight line with the barely distinguishable paracone and metacone; strong development of the parastyle causes the anteroposterior elongation of the tooth. There is a small protocone anterolingual to the paracone and connected to it by a short crest.

Table 2.-Maximum anterior-posterior lengths (in mm) of lower deciduous teeth (plus $\mathrm{M}_{1}$ and $\mathrm{M}_{2}$ where preserved on these jaws) of Moropus elatus and Moropus sp. (from St. Gérand Le Puy, France; Coombs, 1974).

|  | CM | CM | AMNH | AMNH | Moropus |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Measurements | 1755 | 1759 | 86,098 | 86,099 | sp. |
| Length $\mathrm{dp}_{2}$ | - | 14.4 | - | 14.3 | 14.0 |
| Length $\mathrm{dp}_{3}$ | 26.4 | 28.2 | 27.2 | 27.6 | broken |
| Length $\mathrm{dp}_{4}$ | 29.2 | 29.2 | 29.4 | - | 20.5 |
| Length $\mathrm{dp}_{2}$-dp | 67.4 | 70.8 | - | $69.5^{2}$ | 54.2 |
| Length $\mathrm{M}_{1}$ | 35.3 | 35.1 | - | - | - |
| Length $\mathrm{M}_{2}$ | - | 46.7 | - | - | - |

${ }^{a}$ Approximate value.

Posterior and lingual cingula are strong, but there is no anterior cingulum.
A relatively large number of mandibles with deciduous teeth are available for this species. $\mathrm{Dp}_{4}$, though considerably smaller than $\mathrm{M}_{1}$, is strongly molariform. Its metaconid and metastylid are clearly separate at the tips, and in unworn specimens a small paraconid tip is visible; this anterior cuspid is rapidly worn away, however, as the trigonid of $\mathrm{dp}_{4}$ is compressed against the talonid of $\mathrm{dp}_{3}$. Both trigonid and talonid basins are well defined, the latter slightly larger and deeper than the former. $\mathrm{Dp}_{3}$, although more molariform than its permanent counterpart, differs in several respects from $\mathrm{dp}_{4}$, particularly in the trigonid. Although the tooth retains the double crescent shape of the molars and both trigonid and talonid basins are present, the former is very shallow. Compared to the talonid, the trigonid is very narrow, and its paralophid is elongated so that the paraconid lies well anterior to the protoconid. On $\mathrm{dp}_{3}$ the paraconid is almost as strongly developed as the protoconid and is not worn down rapidly. Thus the talonid of $\mathrm{dp}_{3}$ is similar to that of $\mathrm{dp}_{4}$ and the permanent molars, while the trigonid more closely resembles the permanent $\mathrm{P}_{3}$. Metaconid and metastylid are separated at their extreme tips, and the cingula are like those of molars. The small $\mathrm{dp}_{2}$ is in most specimens strongly worn (AMNH 86,099 retains it in good condition, see Fig. 6). It is not at all molariform and strongly resembles the permanent $\mathrm{P}_{2}$. Paraconid, protoconid (the tallest cuspid), and hypoconid are in a straight anteroposterior line. A well-defined crest joins the paraconid and protoconid. Although neither metaconid nor entoconid is visible, there is a trace of a talonid basin on $\mathrm{dp}_{2}$ that is not present on $\mathrm{P}_{2}$.

## Skulls (see Fig. 3)

Holland and Peterson (1914) gave some details of the cranium of CM 2103, a well-preserved (although dorsoventrally crushed) specimen of a large individual from the Agate Quarries. Some of the subsequently recovered material in the American Museum of Natural History shows remarkable preservation of the basicranium, and an M. elatus skull (AM 9923) has also recently been excavated from Morava Ranch Quarry. Comparison of all these skulls with later North American specimens should be profitable when all the material is fully prepared. There are a number of similarities among M. elatus skulls to those of Chalicotlucrium (Filhol, 1891; Colbert 1934) and Borissiakia (Borissiak, 1946), which illustrates the basic unity of cranial structure among all chalicotheriids. Among general chalicothere features are the arrangement of basicranial foramina, the extension of the flat glenoid fossa onto the ventral surface of the zygomatic arch, the partial but not complete posterior closure of the orbit, and the presence of a long medial ventral crest from the internal nares through the presphenoid.

The lateral view of the skull of AMNH 14.375 figured by Coombs (1978) shows uncrushed skull proportions of $M$. elatus and reconstructs the edentulous premaxilla in position. The gently curved dorsal surface of the skull of $M$. elatus lacks any suggestion of doming or elaboration. The stylomastoid foramen, anterior to the base of the paroccipital process and posterior to the enclosed auditory tube, was not mentioned by Holland and Peterson. The condylar foramen of Holland and Peterson is more usually termed the hypoglossal foramen (see Sisson and Grossman, 1953:72). In all cases the bullae are large and rounded, but the paroccipital processes. although well developed, are variable. In some cases (CM 2103) they are concave anteriorly and convex posteriorly, but in other specimens the exact reverse is true. Of particular note in M. elatus is the consistent position of the internal nares and the infraorbital foramina in all specimens examined. In adult individuals the palatines extend posterior to $\mathrm{M}^{3}$, and the internal nares are therefore posterior to $\mathrm{M}^{3}$ also, at least no farther forward than the hypocone of $\mathrm{M}^{3}$. Infraorbital foramina lie on the snout opposite the anterior part of $\mathrm{M}^{2}$.

## Mandibles

Holland and Peterson compared lower jaws of $M$. elatus to those of Equus and Ancylotherium. With
a few minor differences, mandibles of $M$. elatus are very similar to those of other Moropus species. Basic features of the mandible are 1) a narrow anterior part with a short symphysis ending opposite or anterior to $\mathrm{P}_{2}, 2$ ) a long (about as long as and often longer than the premolar row), curved diastema between $I_{3}$ and $P_{2}$ with the mental foramen (sometimes two) lying slightly posterior to its midpoint, 3) base of $P_{2}$ raised somewhat above the level of the diastema, 4) labial and lingual sides of jaw primarily flat but slightly convex below cheek teeth, 5) base of ascending ramus broad, rugose, 6) coronoid process curved posteriorly with long anteroposterior extent, 7) articular condyle flat dorsally with dorsal and posterior parts meeting at almost a right angle, 8) temporal fossa somewhat and pterygoid fossa more strongly excavated, 9) dental foramen large, and 10 ) angle narrow, flat, not projecting notably below the remainder of the jaw margin.

## Vertebrae and Ribs

Vertebrae and ribs of $M$. elatus were described in great detail by Holland and Peterson (1914) and will not be described here. Trends in Moropus cervical vertebrae from II-VII include a very gradual shortening of the centrum, elongation, narrowing, and increased anterior slant of the neural spine, a decrease in the ventral keel, and a slight increase in width but simplification of the transverse process. Between cervical VI and VII the vertebrarterial canal is lost. General chalicothere characters of the cervical vertebrae are elongated centra, oblique anterior and posterior facets on the centra, and a strongly developed ventral keel on anterior vertebrae.

Twenty-one dorsal vertebrae are present in $M$. elatus. Of these, 15 bear ribs (XV has an anterior but no posterior caput facet): I-XV represent thoracics and XVI-XXI lumbars. Some trends represented along the course of the dorsal vertebrae are the following: 1) the neural spine increases in length from I-III, decreases from IV-XIII, then increases again into the lumbar series from XIII-XIX and decreases again from XIX on; 2) the neural spine slants progressively more posteriorly from VIXIII, but then decreases its angle from the vertical to stand almost erect at the last thoracic (XV), and then is nearly straight or very slightly anterior or posterior slanted through the lumbar series; 3) the ventral keel decreases along the most anterior dorsals; 4) there is an increase in the transverse process and separation of a metapophysis from dorsal V


Fig. 7.-Lateral views at scaled size of $M$. elatus scapulae of a small individual (?female), CM 1700, on left, and a large individual (?male), CM 1604, on right. Modified from Holland and Peterson (1914, Fig. 76 and pl. 65).
onward; 5) from VI-XV the exit notch for the spinal nerve forms a progressively larger bony circle; 6) the neural spine becomes less laterally compressed from IV-XII but more compressed from XII onward; 7) the prezygapophyses migrate onto welldeveloped metapophyses from XVI onward, whereas the postzygapophyses of these vertebrae are directed more laterally; 8 ) the centrum becomes less triangular and more oval and dorsoventrally compressed from XIX-XXI.

Well-preserved sacra show fusion of five vertebrae; the transverse processes of the anterior four are enlarged and strongly fused together to form a strong attachment to the ilium. The first sacral is especially broad. The neural spines, which are tightly fused together, become progressively more posteriorly slanted, whereas the size of the centrum decreases as you follow the sacral series posteriorly. The metapophyses on sacral I bear an articular surface for the posteriormost lumbar, but posterior to sacral I they decrease in size and disappear.

No caudal vertebrae are known for any Moropus species outside M. elatus, but several belonging to
M. elatus are preserved, some fused to the sacrum. Known specimens all suggest a small, short tail.

## Forelimb

Scapula.-All M. elatus scapulae are quite similar in general structure. Care must be taken in assessing morphological differences, for here in particular many structural variations are the result of differential allometric growth in animals of different absolute size, either different sexes or growth stages. An example of the differences between scapulae of the same species is shown in Fig. 7, individuals referred by Holland and Peterson to different species. In the larger specimen the tuber spinae is heavier and more posteriorly curved and the upper posterior border of the infraspinous fossa is more rounded, thick, and rugose-adaptations to greater weight bearing (see Osborn, 1929:740-741) in the larger heavier animal.

Scapulae have the following general features: 1) a circular to oval glenoid fossa with a moderately developed coracoid process just anterior to it; 2) an indented anterior border below the spine; 3) ante-


Fig. 8.-Dorsal (A) and volar (B) views (excluding trapezium, pisiform) of right carpus of AMNH 14,378, M. elatus, from the Agate Spring Quarries, Sioux Co., Nebraska. Labels in Fig. 9.
rior border of blade slightly more convexly rounded than posterior border; 4) upper (proximal) end slightly squared to gently rounded; 5) well-developed spine with posteriorly reflected tuber spinae: 6) supraspinous and infraspinous fossae of subequal size; 7) subscapular surface gently concave with a slightly convex ridge in the anterior or middle part. M. elatus has a more strongly posteriorly reflected tuber spinae than is known in other Moropus species.
Humerus (Fig. 13A).-The humerus of Moropus, unlike the femur, is not easily confused with humeri of contemporary perissodactyls (for example, of rhinoceroses). Compared to the probable weight of the animal and the size of the proximal articulation and greater tuberosity, the shaft is very long. Even more unusual is the comparatively strong development of the entepicondyle, otherwise reduced or absent in all but the most primitive ungulates. The distal trochlea is transversely very broad and is not
deeply grooved; the anterior part of the trochlea (capitulum), with which the radius articulates, is particularly wide. Holland and Peterson (1914:334335) mentioned the following important features of the humerus of $M$. elatus: large, rounded head; well, but not unusually, developed greater tuberosity; relatively shallow but broad bicipital groove; prominent deltoid ridge extending well down the shaft and flexed posteriorly; prominent ectocondylar ridge (but not as strong as in most other perissodactyls); deep olecranon fossa; shallow coronoid fossa; plus the very important characters of the distal end mentioned above.

Radins-illna.-Although a number of radii and ulnae are available, there are few consistent differences from other Moropus specimens, which can be regarded as of taxonomic value. In many cases only a single radius or ulna (often broken) is known; in other cases the two bones are solidly fused, usually at the distal end and sometimes also for part of


Fig. 9.-Labeled drawing of dorsal and volar views of right carpus of AMNH 14,378 shown in Fig. 8.
the shaft. There does not seem to be any quarry or locality correlation between groups in which more or less fusion occurs; rather, fusion may be correlated with the age of the animal. Whether or not strong fusion occurred does not seem to be functionally critical, for in any case the facets between the two bones at their proximal ends would allow little or no movement between them, certainly no rotation of the radius.

General features of the ulna include rather short but heavy olecranon process, prominent anconeal process, deep semilunar notch with strong expansion near the radius facet, radius facet distal and at an acute angle to semilunar notch and forming a deep articular fossa, shaft subtriangular in section, distal end narrow with cuneiform facet flat and adjacent (across a 90 -degree arc) to the pisiform facet on the posterior (volar) surface. Some radius features include proximal and distal ends broader than shaft articular surface for humerus with broad, slightly concave ulnar (lateral) part and narrower, flatter radial (medial) part, coronoid process weak, facet for ulna with proximally oriented central
tongue and posteriorly (volar) oriented radial and ulnar parts (somewhat variable), distal end with dorsal groove between scaphoid and lunate facets, lunate facet more concave and of greater dorsovolar extent than scaphoid facet.

Carpals.-Carpal elements of M. elatus were described and figured by Holland and Peterson (1914:337-339), but additional material has given a more accurate view of the absence of significant variation among specimens and the general usefulness of manus and pes elements in taxonomy. Therefore the most salient features of the carpals are worth rediscussing here as a basis for taxonomic and functional work to follow (see Figs. 8-12).

On the scaphoid the weakly convex articular surface for the radius covers all of the proximal surface except for a rugose protuberance at the ulnovolar angle (Fig. 10A). The radiovolar surface bears a small but well-defined, distally slanting, convex facet for the trapezium (Fig. 8B). Adjacent and distal to the trapezium facet is the saddle-shaped trapezoid facet, a large facet, which reaches distally onto the radial side of the distal process (Fig. 10B, pal-


Fig. 10.-Proximal ( A and C with radial edge at right) and distal ( B and D with radial edge at left) views of right cuneiform, lunate, scaphoid (A, B) and right unciform, magnum, trapezoid (C, D) of M. elatus, AMNH I4,378, from the Agate Spring Quarries, Sioux Co., Nebraska. Abbreviations for facets in Figs. I0-12, 22, and 24-26 are as follows: R, radius; U, ulna; P, pisiform; S, scaphoid; L, lunate; Cn, cuneiform; Un, unciform; M, magnum; Td, trapezoid; Tm, trapezium; II, Mc II; III, Mc III; IV, Mc IV; V, Mc V.
mar process of Holland and Peterson). Of the two facets for the lunate on the ulnar surface (Fig. 11A), the proximal oval one stands on a low platform and is particularly prominent at its volar edge. The more distal lunate facet occupies the ulnar surface of the distal process and curves from the magnum facet in a proximoulnar direction so that in its most proximal part it borders the volar edge of the trapezoid facet. Between proximal and distal lunate facets, the ulnar surface of the trapezoid is depressed. Because the large distal process is squared, the facet for the magnum on its distal end is flat to slightly convex, bordered on one side by the trapezoid facet and on the other by the distal lunate facet.

On the lunate, the proximal articulation, which is for the radius, is of suboval shape and convex in
all directions, especially strongly so in the dorsal to volar direction (Fig. 10A). Very prominent in a proximal view is the volar process near the distal edge, which has a facet (for the magnum) on its distal but not on its proximal surface (Fig. 10B). Of the two scaphoid facets on the radial surface (Fig. 11 B ), the proximal one is large and adjoins the radius facet across a prominent keel; separated by a groove from the proximal facet, the distal scaphoid facet varies slightly in position in different specimens, sometimes passing along the radiodistal surface of much of the volar process but barely distinguishable from the magnum facet except on the volar process. On the most distal part of the radial surface of the lunate, the magnum facet curves onto the distal surface of the volar process, where it


Fig. 11.-A) Ulnar view of right scaphoid, trapezoid, and Mc II (dorsal edge at right), and B) radial view of right lunate, magnum, and Mc III (dorsal edge at left) of M. elatus, AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska. See Fig. 10 for facet abbreviations. Unlabeled line points to volar process of lunate.
forms a concave, cup-shaped facet separated by a ridge from the distal lunate facet (Fig. 10B). All along its most distal and ulnar edges the magnum facet is divided by a beak-like ridge from the unciform facet (Figs. 10B, 12A). The unciform facet has two parts, the dorsal part flat to convex and with an almost entirely distal orientation, the volar adjoining part slightly concave and curving onto the ulnar side of the bone, where it is weakly distinguishable from the cuneiform facet. Flat to weakly convex and on a low platform, the cuneiform facet forms a D-shaped tongue onto the ulnar surface of the lunate (Fig. 12A).

Several cuneiforms from the Agate Quarries and Morava Ranch Quarry were compared with YPM 24,632, which is part of the type collection of $M$. elatus and closely resembles the more recently collected specimens. This bone is very deep in the dorsal to volar direction but is transversely narrow. At the dorsoradial angle and volar edge the cuneiform tapers to a blunt point, giving the bone a wedgeshaped appearance in proximal view (Fig. 10A). The dorsal and ulnar surfaces of the bone are rough, but not strongly rugose, and on the distal part of the ulnar surface is a blunt roughened protuberance
for the attachment of muscles or ligaments (Figs. $8 \mathrm{~A}, 10 \mathrm{~B}$ ). There is another, smaller protuberance near the proximal edge of the narrow volar surface. Both pisiform and ulna articulate with the proximal surface of the cuneiform (Fig. 10A). The relative amounts of the proximal surface occupied by each varies in the specimens examined, but in each case the more dorsal facet, for the ulna, is larger. A very weak diagonal ridge separates the two facets, and the pisiform facet is raised slightly above the ulna facet. Both facets are wedge-shaped, the slightly concave ulna facet narrowest in the volar direction, the weakly convex pisiform facet narrowest dorsally. On the distal surface of the cuneiform (Fig. 10 B ), the unciform facet is concave in the dorsal to volar direction and closer to the dorsal than to the volar edge of the bone. There is only one, tonguelike facet for the lunate, at the distal edge of the radial surface (Fig. 12B), and adjoining the unciform facet at a right angle. No second, more proximal lunate facet is observable.

On pisiform specimens of M. elatus, the cuneiform facet is parallel to the long axis of the pisiform and the adjacent ulna facet perpendicular to it. Both surfaces curve in tongues away from their straight


Fig. 12.-A) Ulnar view of right lunate, magnum, and Mc III (dorsal edge at right), B) radial view of right cuneiform, unciform, and Mc IV (dorsal edge at left), and C) proximal view of right Mc IV, Mc III, and Mc II (dorsal edge below, radial edge at right) of $M$. elatus, AMNH 14,378, from the Agate Spring Quarries. Sioux Co., Nebraska. See Fig. 10 for facet abbreviations.
adjoining edge, each slightly concave, but the ulna facet more so. When placed in articulation with the cuneiform, the pisiform does not occupy the entire pisiform facet on the cuneiform and so may have been capable of some dorsovolar movement against the cuneiform. The part of the pisiform on which the articular facets lie is expanded in all directions, but volar to that region the pisiform is laterally constricted; still farther in the volar direction the pisi-
form is expanded and rugose for muscle attachment, its end slightly curved in the radial direction.

The unciform (hamate) has two prominent processes, a dorsoradial one and an ulnovolar one. Of these, the former is near the proximal edge of the bone and the latter near the distal edge (Figs. 10C, D). There are two facets on the proximal surface (Fig. 10C), the more distal and radial for the lunate and extending onto the above-mentioned dorsora-
dial process. On its radial side (Fig. 12B), this primarily concave facet adjoins the much smaller magnum facet at a right angle; its volar edge borders the cuneiform facet along a blunt ridge. The cuneiform facet is strongly convex in the dorsal to volar direction and curves onto the volar side of the bone (Fig. 8B). This facet is much larger than the corresponding facet on the cuneiform, so that during flexion of the carpus the unciform was able to move considerably with the result that the volar surface of its cuneiform facet was then in contact with the cuneiform. No facets are present on the roughened ulnar surface of the unciform, for Mc V does not articulate with the unciform. On the radial side of the unciform are two facets (Fig. 12B). The proximal one, for the magnum, has a trapezoidal shape and flat surface and lies on a very weak, distally slanted platform, with the radial surface of the unciform roughened and depressed on either side of it. Generally speaking, the platform for the magnum facet is more pronounced in specimens from Morava Ranch Quarry than in those from the Agate Quarries. There is also variably present in M. elatus (absent in Fig. 12) a narrow volar extension of the magnum facet adjoining the lunate facet. The trapezoidal magnum facet indistinctly borders the facet for Mc III, which in turn indistinctly borders the Mc IV facet near the distal edge of the radial surface of the unciform (visibility and location of Mc IIIMc IV facet boundaries vary somewhat among specimens). The weak ridge, which appears to separate the Mc III facet from the Mc IV facet, is actually shared by both facets. The Mc III facet varies in its dorsal to volar extent but in any case does not reach as far in the volar direction as does the Mc IV facet, which occupies the distal surface of the ulnovolar process (Fig. 10D).

Although the magnum is one of the largest bones in the carpus, only a small part of it is visible in dorsal view; it is most strongly developed in its volar part. The largest of the four facets visible from the radial side (Fig. 11B) is that for Mc II, irregular in shape and slightly concave. There are two facets for the trapezoid, a larger dorsal one between scaphoid and Mc II facets and passing onto the proximal surface of the magnum, and a smaller oval-shaped volar one also near the proximal edge (it borders proximally parts of both scaphoid and lunate facets). Of the two large curved facets on the proximal surface of the magnum (Fig. 10C), the more dorsal one articulates with the distal process of the scaphoid. Most of the volar part of the prox-
imal surface is occupied by a convex, ball-shaped lunate facet, which fits into the cup of the volar process of the lunate. The dorsal part of the lunate facet curves onto the ulnar surface of the magnum and is separated by only a weak ridge from the unciform facet. Compared with adjoining facets, the unciform facet is small and flat, lying on a low platform (Fig. 12A). It attains the distal edge of the ulnar side of the magnum where it joins the Mc III facet at right angles. The latter facet, on the distal surface (Fig. 10D), is a very elongated facet, passing in the distovolar direction for nearly the entire extent of the well-developed volar hook. The Mc III facet is irregularly concave along most of its length and may be divided by a dorsal to volar directed ridge into moieties of unequal size.

In both proximal and dorsal views (Figs. 10C, 8A), the trapezoid has a triangular appearance, in the former case the apex being the volar angle, in the latter the distal angle which fits into the proximal groove on Mc II. The entire proximal surface (Fig. 10C) is occupied by the scaphoid facet, concave transversely and convex in the dorsal to volar direction. Curving onto the volar surface of the trapezoid (Fig. 8B), this facet merges into the facet for the trapezium, which occupies most of the volar surface and is continuous with trapezium facets on the scaphoid and Mc II. The scaphoid facet also curves onto the ulnar surface of the trapezoid (Fig. 11 A ), where it borders the two facets for the magnum. The larger dorsal magnum facet has a slight distal slant and a subtrapezoidal shape. Volar to this facet is a rough-surfaced depression, larger than the dorsal facet itself. Only at the extreme proximovolar edge of the dorsal magnum facet, bordering the scaphoid facet, is a small flattened area representing the volar articular facet for the magnum. Separated by a distinct ridge from the dorsal magnum facet is the facet for Mc II. This distal facet, like its counterpart on Mc II, has a V-shape (Fig. 10D), and its radial edge meets the trapezium facet at an acute to right angle on the volar surface of the trapezoid.

A number of trapezium specimens of $M$. elatus are known. This small bone contacts facets on the scaphoid, trapezoid, and Mc II.

Metacarpals.-The "dorsal surface" of Mc II described by Holland and Peterson (1914) is actually a dorsoradial surface (with radiovolar and dorsoulnar processes at either end, see Fig. 12C) when Mc II is placed in articulation with Mc III. For this reason, dorsal of Holland and Peterson is
here called dorsoradial. a term also adopted by Borissiak (1946) and Belyaeva (1954). In dorsoradial view (Fig. 8A) the proximal surface of Mc II is M -shaped, broadened by radiovolar and dorsoulnar processes that extend to either side of the shaft. Most of the radiovolar process is occupied by a well-developed trapezium facet (Fig. 8B), which is weakly concave and widest in its radial part. The trapezium facet is contiguous to, but separated by, a sharp crest from the concave trapezoid facet, which forms the middle V of the above-mentioned $M$ (Fig. I2C). An ulnar crest, which joins the one between trapezium and trapezoid facets to form the apex of a triangle enclosing the trapezoid facet (Fig. 12C), separates the trapezoid facet from the magnum facet. The magnum facet is the last (ulnar) limb of the M and overhangs the Mc III facet (Fig. IIA), which forms the proximal part of a deep concavity on the ulnar side of the bone. On the volar side of the dorsoulnar process the Mc III facet curves distally, so that when Mc II and Mc III are articulated, Mc II covers both dorsoradial and proximoradial parts of Mc III. The shaft of Mc II, almost circular in section. is more massive than that of either Mc III or Mc IV. The distal end is rotated clockwise in relation to the proximal end, having an effect in turn on the orientation of the fused proximal and medial phalanges (bearing the large claw) of this digit. General features of the distal end of Mc II are 1) the strongly developed ulnar tubercle proximal to the phalangeal articular surface, 2) the unequal development of the sesamoid facets. the ulnar facet being wider and extending farther distally than the radial facet, 3) the weakness of the keel between the two sesamoid facets, and 4) the presence of a foramen on the radial surface just proximal to the articular facets. YPM 24.632, a distal end of Mc II, which was part of Marsh's type collection of M. elatus. shows no special differentiating features from Agate and Morava Ranch Quarry material.

Most of the proximal part of the dorsal surface of Mc III is rugose (Fig. 8A), except for a subtriangular area, which articulates with the dorsoulnar process of Mc II. This facet is continuous with the Mc II facet on the proximal surface (Fig. IIB, despite the implication by Holland and Peterson, 1914:350, 352, that the two are separate facets). The proximally oriented part of the Mc II facet extends in a dorsal to volar strip across the radial side of the proximal surface. It is delineated only by a faint ridge from the broader magnum facet, which occupies the middle part of the Mc III proximal sur-

Table 3.-Maximum lengths (in mm ) and ratios of maximum lengths of metacarpals in individuals of selected chalicothere species.

| Specimens | Mc II | Mc III | Mc IV | Mc II Mc III | Mc IV/ <br> Mc III |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Moropus elatus |  |  |  |  |  |
| AMNH 14,378 | 198 | 229 | $200^{\text {a }}$ | 0.86 | $0.87^{\text {a }}$ |
| CM 1700 | $164{ }^{\text {a }}$ | 188 | 166 | $0.87^{\text {a }}$ | 0.88 |
| CM 1604 ${ }^{\text {b }}$ | 230 | 274 | 221 | 0.84 | 0.81 |
| Moropus hollandi |  |  |  |  |  |
| CM 1424 | 174 | - | - | - | - |
| FMNH Pl3000 | 178 | 206 | 190 | 0.86 | 0.92 |
| Schizotherium priscum |  |  |  |  |  |
| Specimen in Paris ${ }^{\text {c }}$ | 115 | 130 | 126 | 0.88 | 0.97 |
| Ancylotherium (A.) pentelicum |  |  |  |  |  |
| AMNH 32504 ${ }^{\text {d }}$ | $234{ }^{\text {a }}$ | 279 | 275 | $0.84^{\text {a }}$ | 0.98 |
| Chalicotherium grande |  |  |  |  |  |
| CM 2298 ${ }^{\text {e }}$ | 163 | 198 | 212 | 0.82 | 1.07 |

a Approximate measurement.
${ }^{\text {b }}$ Measurements taken from Holland and Peterson, 1914.
"An uncatalogued specimen, possibly a composite, from the Phosphorites of Quercy, located in Muséum National d'Histoire Naturelle, Paris.
${ }^{\text {d }}$ Cast of an uncatalogued specimen from Pikermi in the Muséum National d'Histoire Naturelle, Paris.
${ }^{e}$ Cast of specimen from Sansan (Gers), France.
face (Fig. 12C). Along its dorsal to volar axis the magnum facet is concave in its dorsal part and convex in its volar part, extending farther in a volar direction than any other part of the proximal surface. A sharp crest separates the magnum facet from that for the unciform, which adjoins it in the ulnar direction. This latter facet is subtriangular with a volar apex and overhangs the facet(s) for Mc IV, separated by another sharp crest (Fig. 12A). Despite Holland and Peterson's (1914:353) observation of a double Mc IV facet, divided into two by a sinus, there is often a single, undivided facet. In any case the Mc IV facet(s) occupies ( -y ) the proximal surface of a large concavity on the ulnar surface of Mc III. The shaft of Mc III is subquadrate in section and the distal end is only slightly asymmetrical. A blunt ridge continues distally from the Mc II facet along the dorsoradial angle for about half the length of the shaft.

Mc IV is oriented so that what seems to be a flat dorsal surface (Fig. 8A) actually has a dorsoulnar orientation when the bone is articulated with Mc III, a situation the opposite of that for Mc II. Of the two Mc III facets (Fig. 12B, or parts of a single,
undivided facet), the largest and most convex is the dorsal one, whereas the smaller volar facet has a less proximal and more completely radial orientation. Separated from the Mc III facet(s) by a weak to somewhat pronounced rib, the unciform facet occupies almost all of the proximal surface of Mc IV and is subtriangular with a volar apex (Fig. 12C). An important feature of Mc IV is its articular surface for Mc V , the reduced metacarpal that articulates with no other bone. This articulation is on the ulnovolar angle of Mc IV (Fig. 8B) and is separated from the proximal edge by paired tubercles (one ulnar, one volar). The Mc V facet is on the distal volar surface of the ulnar tubercle. The shaft of Mc IV becomes more oval and less triangular in section distally. Mc IV is less symmetrical than Mc III, but more so than Mc II, and at its distal end the radial tubercle is larger than and proximal to the ulnar one, whereas the ulnar of the two sesamoid facets is smaller.

In M. elatus Mc V has a two-part Mc IV facet on the dorsoradial side of its proximal end and a transversely compressed shaft. Small sesamoid and phalangeal facets are present on the distal end, which reaches the level distally of the proximal end of sesamoid facets in Mc IV. In articulation with Mc IV, Mc V was somewhat volar to the other metacarpals and was strongly divergent at its distal tip from the remainder of the manus.

Manus summary.-A complete analysis of the manus is best taken as part of a broad functional study of Moropus (Coombs, in preparation), but a few comments are useful. Despite the lack of rotation ability at the wrist (see radius-ulna comments), carpal facets suggest that the wrist was quite flexible from side to side and that strong flexion was possible along two planes, at the ulnocarpal joint and between the proximal and distal rows of carpals. Manus flexion in M. elatus was not so pronounced, however, as in Ancylotherium (Ancylotherium) pentelicum (Schaub, 1943), where the trapezium was lost and the scaphoid could contact Mc II during extreme flexion. Weight was borne primarily by the distal ends of the metacarpals, with participation by the sesamoids and the proximovolar ends of proximal phalanges. Except for the tips of the ungual phalanges, the hooked digits were probably held clear of the ground during walking by hyperextension of the proximal phalanx and flexion of the other phalanges (see digit II of manus in Fig. 2). Mc III and Mc IV are almost the same length, but weight was concentrated on the more symmet-
rical Mc III. The torsion and other unusual features of the relatively short Mc II are associated with the bearing of the large hooked claw by this digit.

## Hindlimb

Innominate.-Complete pelvis specimens are otherwise rare in Moropus but are well known in M. elatus. Chalicothere features not shown so strongly in other perissodactyl innominates are the longer and narrower pelvic proportions, primarily because of expansion of the ischium and pubis posterior to the acetabulum and the fairly long shaft of the ilium. Articulation with the femur and relations to the sacrum and lumbar vertebrae suggest that the ilium was nearly vertical in the living animal, although probably not so sharply vertical as it was mounted by Osborn (AMNH 14,375, Fig. 2). On the medial surface of the ilium, the articular surface for the sacrum is heavy and rather long. The iliac crest is expanded but not strongly so. Aside from the rugosities along the iliac crest, there is an obvious rugose area of muscle attachment (for the rectus femoris) just anterior and dorsal to the acetabulum. The acetabulum is deeply excavated with a heavy dorsal overhang, which aided in supporting the body over the femur.

Femur (Fig. 13B).—Holland and Peterson (1914), while describing the femur of M. elatus, compared and differentiated it from the femur of titanotheres. Actually the greatest problem in the identification of Moropus femora is in comparison with those of rhinoceroses found in beds of the same age, usually in greater numbers. Features, which usually differentiate a Moropus femur, are 1) the symmetrical or nearly symmetrical (less symmetrical in older individuals), slightly oblique patellar facet (that in rhinos is more asymmetrical), 2) the asymmetrical development of the distal condyles, the medial condyle extending farther posteriorly (condyles of contemporary rhino femora are more nearly symmetrical), 3) the lesser development of the third trochanter, and 4) the very small but persistent $f o$ vea capitis on the head for attachment of the ligamentum teres (the fovea on rhinoceros femora is usually larger).

The large number of known M. elatus femora are essentially similar in morphology, although there is some individual variation in the proportional width of the shaft. In larger femora of M. elatus, the shaft is relatively broader. Weight-bearing adaptations such as this, in a species where size variation is as great as in M. elatus, suggest that one must be care-


Fig. 13.-Anterior views of A) distal end and shaft of left humerus, B) right femur, C) patella, and D) left tibia of M. elatus, AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska. Abbreviations: D.r., deltoid ridge; C.f., coronoid fossa; Cap, capitulum; Ent, entepicondyle; Ect, ectocondylar ridge: 1, greater trochanter (broken); 2, lesser trochanter; 3, third trochanter; Pat, patellar facet; Cnm, cnemial crest; Mm, medial malleolus; F, fibula articulations.
ful in drawing specific boundaries on the basis of proportions alone. In addition to the characters cited above, $M$. elatus femora share well-developed greater and lesser trochanters and a fairly deep trochanteric fossa. Distal to the third trochanter, the shaft narrows quite abruptly and then broadens close to the distal end.

Tibia and fibula.-Among known Moropus species, the fibula has been preserved only in M. elatus: it will not be discussed further here. Tibiae vary little in proportions and morphology, and there is therefore little to add to the description of Holland and Peterson (1914:363). Some of the most prominent features are (Fig. 13D): 1) a heavy cnemial crest, which is rugose proximally and extends a good distance distally along the shaft, 2 ) two broad
proximal articular surfaces for the condyles of the femur, of which the lateral surface is slightly more curved, 3) a $V$-shaped or double (spreading apart anteriorly) spine between the two femur articular surfaces, with the medial side of the spine sharper and taller, 4) well-developed articular surfaces both proximolaterally and distolaterally for the fibula and a well-defined ridge for the interosseous ligament connecting the proximal and distal facets, and 5) a strong medial malleolus. There is no evidence that the medial malleolus contacted the calcaneum during extreme flexion as Holland and Peterson suggested.
Patella (Fig. 13C).-Patellae are not known for all Moropus species, but there is some evidence of differences among species. Patellae of M. elatus

Table 4.-Measurements (in mm) of astragali of selected chalicothere specimens, including proportions of tibial height/maximum width.

| Taxa and specimens | Maximum width | Height of tibial side ${ }^{\text {a }}$ | Height width |
| :---: | :---: | :---: | :---: |
| Moropus elatus. <br> AMNH $14378^{\text {b }}$ | 89.9 | 74.7 | 0.83 |
| Moropus elatus, CM $1701^{\text {b }}$ | 76.7 | 68.8 | 0.86 |
| Moropus elatus. <br> AM $9722^{\circ}$ | 89.7 | 68.8 | 0.77 |
| Moropus elatus. <br> AM 9723 ${ }^{\circ}$ | 92.9 | 74.5 | 0.80 |
| Moropus elatus, <br> AM $9724^{\circ}$ | 90.8 | 71.2 | 0.78 |
| Moropus elatus. <br> Range of six Frick Morava Ranch Quarry specimens | $81.1-98.0$ | 62.5-77.2 | 0.77-0.82 |
| Moropus hollandi. <br> CM $1424^{\text {d }}$ | 84.1 | 64.0 | 0.76 |
| Moropus hollandi, <br> F:AM $54,902 \mathrm{~g}$ | 103.5 | 74.4 | 0.72 |
| Moropus merriami, <br> UCMP 11,605 | 100.7 | 64.9 | 0.64 |
| Moropus inerriami, UCMP 19,404 | 102.6 | 62.2 | 0.61 |
| Schizotherium turgaicum ${ }^{\text {a }}$ | 43.5 | 38.5 | 0.89 |
| Schizotherium turgaicum ${ }^{\text {e }}$ | 47 | 41 | 0.87 |
| Borissiakia betpakdalensis ${ }^{\text {s }}$ | 92 | 74 | 0.80 |
| Borissiakia betpakdalensis ${ }^{\text { }}$ | 68 | 58 | 0.85 |
| Ancylotherium <br> (Metaschizotherium) fraasi ${ }^{8}$ | 83.4 | 56.0 | 0.71 |
| Chalicotherium rusingense ${ }^{\mathrm{h}}$ | 66.0 | 35.7 | 0.54 |
| Chalicotherium salimum, <br> AMNH 19,436 | 88.6 | 37.7 | 0.43 |
| Chalicotherium grande. CM 2299 (cast) | 100.7 | 41.2 | 0.41 |
| Chalicotherium grande ${ }^{\mathrm{h}}$ | 100.5 | 46.2 | 0.46 |
| Chalicotherium goldfussi ${ }^{\text {b }}$ | 98.7 | 44.7 | 0.45 |

${ }^{\text {a }}$ Height measurement includes neck and edge of navicular facet.
${ }^{\text {b }}$ From Agate Spring Quarries, Sioux County, Nebraska.
${ }^{\text {c }}$ From Morava Ranch Quarry, Box Butte County, Nebraska.
${ }^{\text {d }}$ Holotype, right side.
${ }^{e}$ Taken from Belyaeva, 1954:57-58.
${ }^{\mathrm{f}}$ Taken from Borissiak, 1946.
${ }^{\mathrm{g}}$ Taken from von Koenigswald, 1932.
${ }^{\mathrm{h}}$ Taken from Butler, 1965.
have 1) the facet for femur not so wide transversely as tall, 2) the trochlear ridge between the two sides of the femur facet blunt, with curved sides of the facet at obtuse angles to one another, 3) the anterior
patellar surface rugose with some but not strong development of a proximal ridge for the insertion of knee extensors, and 4) a distal tongue developed at the patellar apex (except in one Morava Ranch Quarry specimen). It is important to note that YPM 24,632, a patella, which was part of Marsh's type collection of M. elatus and first figured by Holland and Peterson (1914:223), is like the majority of patellae of M. elatus.
Tarsals (Figs. 14-17).-In all astragali of M. elatus a small neck distal to the trochlea is present (Fig. 14C), on whose distal surface the large navicular facet lies. The neck is most pronounced on the tibial side of the bone, in some specimens very pronounced, but it may be reduced at its fibular edge (distal to the middle part of the astragalar trochlea). Over half the width of the astragalus is occupied by the fibular side of the trochlea, which is more gradually slanted than the tibial side. The fibular edge of the trochlea does not ascend proximally quite so far as does the tibial edge, and distally it hangs free from the rest of the bone (but does not extend farther distally than the navicular facet). On the volar surface of the astragalus (Fig. 14B), the most obvious feature is the deeply concave ectal facet for the calcaneum, which extends more than half the transverse width of the astragalus as well as over half the height. The ectal facet is rather uniformly concave from proximal to distal throughout its width. A sharp proximal ridge separates the ectal facet from the dorsal surface of the trochlea. Distally, across a blunt ridge along the fibular half of its width, the ectal facet borders the smaller, weakly convex calcaneal facet, also for the calcaneum. The latter facet is slanted strongly in a distal direction and away from the ectal facet. Both ectal and calcaneal facets are separated by a rugose area containing nutrient foramina from a third facet for the calcaneum, the sustentatucular facet, on the tibiodistal side of the astragalus' volar surface. The sustentacular facet is generally oval in shape, weakly convex, and lies flat on the plane of the volar surface. On the distal surface of the astragalus the single facet for the navicular is distinctly pear-shaped with a narrow fibular end. Weakly convex transversely and at its fibulovolar angle, the facet passes slightly onto the fibular and volar surfaces of the astragalus, but along its entire dorsal edge a distinct ridge separates it from the dorsal surface.

The tuber calcis of the calcaneum is long and massive, with a subtriangular cross-section. Its dorsal surface is narrower than its rugose volar surface,


Fig. 14.-A) Dorsal view right calcaneum, B) volar view right astragalus, C) dorsal view right tarsus, and D) volar view right tarsus of AMNH 14,378 (missing mesocuneiform and entocuneiform), M. elatus, from the Agate Spring Quarries, Sioux Co., Nebraska. Tarsus elements identified in Fig. 15; facets on astragalus and calcaneum abbreviated as follows: E, ectal; S, sustentacular; C, calcaneal.


Fig. 15.-Labeled drawing of dorsal and volar views of tarsus of AMNH 14,378 shown in Fig. 14.
and the end of the tuber, where there is a pronounced rugose area for muscle attachment particularly characteristic of this species (Fig. 14D), is thicker than the shaft. Of the facets for the astragalus (Fig. 14A), the ectal facet is relatively narrow but extends well onto the dorsal surface of the tuber. Here it is only weakly convex, but distal to the tuber it forms a protruding right-angle bend corresponding to the deeply concave ectal facet on the astragalus. On some specimens there appears to be a facet for the tibia at the edge of the ectal facet on the tuber (mentioned by Holland and Peterson, 1914:366, although no particular evidence for it exists on the tibia). In those specimens where such a facet exists, the ectal facet, rather than being flat on the tuber, is raised on a platform so that the tibia facet is continuous with the astragalar trochlea when the astragalus and calcaneum are articulated [also noted in Ancylotherium (A.) pentelicum]. The oval, slanted sustentacular facet occupies almost the entire sustentacular process and is separated
from the ectal facet by a groove for the interosseous ligament. The third facet, corresponding to the calcaneal facet on the astragalus, is distal to the ectal facet on what Holland and Peterson termed the "lesser process," which is well developed. On the distal end of the calcaneum is the pear-shaped cuboid facet, flat on its fibular side and slightly concave on its tapering tibial side. There is no facet on the narrow distal surface of the sustentacular process. The paralectotype of M. elatus, YPM 24.631, includes a broken calcaneum. Although retaining only the tuber calcis, it can without question be connected with the other specimens here described. Important common features are the strong rugose protuberance at the end of the tuber calcis and the shape of the ectal facet as it extends onto the tuber.

On the cuboid, the calcaneum facet is pearshaped (Fig. 16E), corresponding exactly to the distal facet on the calcaneum. It occupies the entire proximal surface and is set off by a ridge from the remainder of the bone; articulation with the calca-


Fig. 16.-Tibial (A - C , proximal edge at top) and proximal (D - F, dorsal edge at bottom) views of cuboids of $M$. hollandi (A, D, left cuboid), FMNH P13000, from near Jay Em, Goshen Co., Wyoming; M. elatıs (B, E, left cuboid), AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska; and M. distans (C, F, right cuboid), YPM 24.628, from Bridge Creek, Oregon. Distal views (dorsal edge at bottom) of naviculars of G) M. hollandi, FMNH P13000, and H) M. elaths, AMNH 14,378. Facet abbreviations used in Figs. 16-I9 and 27-28 are as follows: Ca, calcaneum; Cu, cuboid; N, navicular; Ec, ectocuneiform; Me, mesocuneiform; II, Mt II; III, Mt lli ; IV, Mt IV.
neum is slightly oblique. The dorsal, fibular, and most of the volar surfaces of the cuboid are gently curved and relatively smooth, but at the tibiovolar angle is developed a strongly rugose process for muscle attachment, which overhangs Mt IV (Figs. 14D, 16B, 17C). The tibial side of the cuboid (Figs. $16 \mathrm{~B}, 17 \mathrm{C}$ ) has no articular surface in its most proximal and volar parts, where it is separated from the navicular by a small space. The navicular facet lies in a dorsal to volar strip, which occupies one-third of the height of the tibial surface and lies about halfway between the proximal and distal edges of the bone. This facet is slanted to form the proximal
part of a V of which the ectocuneiform facet is the distal part. Occupying the most distal part of the tibial surface, the ectocuneiform facet consists of dorsal and volar divisions, which may or may not be separate. The distal surface of the cuboid, except for the tibiovolar process, is occupied by the large quadrilateral facet for Mt IV, weakly concave except near its tibiovolar angle where it is convex.

The proximal facet of the navicular is transversely concave, particularly at its tibiovolar angle, where it follows the curve of the corresponding facet on the astragalus (Figs. 14C, 17B). Three other facets are visible on the distal surface (Figs. 16H,


Fig. 17.-Views of right tarsals and metatarsals of $M$. elatus, AMNH 14,378 , from the Agate Spring Quarries, Sioux Co., Nebraska: A) Tibial view of navicular, ectocuneiform, and Mt III (dorsal edge at left); B) fibular view of navicular, ectocuneiform, and Mt III (dorsal edge at right); C) tibial view of cuboid and Mt IV (dorsal edge at left); D) proximal views of Mt IV, Mt III, and Mt II (dorsal edge at bottom). Facet abbreviations as in Fig. 16.

17A, B). Of these, the cuboid facet (fibularmost) does not abut the astragalus facet and is like a short dorsal to volar bar (like the corresponding facet on the cuboid). The ectocuneiform facet is about two times as large as that for the mesocuneiform (the most tibial of the distal facets) and has an irregular surface (primarily convex in a dorsal to volar direction) and shape (broadest dorsally and tapering in the volar direction). A shallow groove near the vo-
lar edge of the ectocuneiform facet to accommodate a weak ridge of the ectocuneiform prevents dorsal to volar movement of the navicular and ectocuneiform against one another. The irregularly curved, weakly convex mesocuneiform facet is slanted to approach on its tibial side, but not adjoin, the facet for the astragalus. Weak ridges between the three distal facets of the navicular are their only distinguishing boundaries.

Table 5.-Maximum lengths (in mm) of the three metatarsals within single chalicotheriid specimens.

| Specimens or <br> taxa | Length <br> Mt II | Length <br> Mt III | Length <br> Mt IV | Mt II/ <br> Mt III | Mt IV/ III |
| :--- | :---: | :---: | :---: | :---: | :---: |

${ }^{\text {a }}$ Specimens of Moropus elatus from the Agate Spring Quarries, measurements of CM 1706a from Holland and Peterson, 1914.
${ }^{\text {b }}$ Moropus cf. M. hollandi.
${ }^{\text {c }}$ Specimen (possibly a composite) from the Phosphorites of Quercy in the Muséum National d'Histoire Naturelle, Paris.
${ }^{\text {d }}$ AMNH 10.564, cast of specimen from Pikermi in the Muséum National d'Histoire Naturelle, Paris.
${ }^{e}$ CM 2299, cast of specimen from Sansan.

On the proximal surface of the ectocuneiform, the shield-shaped navicular facet is broadest dorsally and occupies all except the volar angle of the bone, where there is a well-developed, rugose volar process (Figs. 14D, 17B). This process closely approaches the larger tibiovolar process of the cuboid when ectocuneiform and cuboid are articulated. There are some differences among ectocuneiform specimens in proportions and in the development of a single or double cuboid facet on the fibular surface. An important feature on the dorsal part of the fibular surface (Fig. 17B), distal to the cuboid facet(s), is a rounded facet for Mt IV, very distinct and continuous with the cuboid facet(s). On the tibial side of the ectocuneiform lie two articular surfaces (Fig. 17A). The proximal one, for the mesocuneiform, is small and flat. It occupies the middle third of the dorsal to volar depth of the ectocuneiform and is delineated from the proximal surface of the bone by a sharp ridge. Distal to this facet and occupying the entire depth of the ectocuneiform is the band-like, slightly convex facet for Mt II. Thus the ectocuneiform of $M$. clatus contacts all three metatarsals. On its distal surface is an irregularly shaped and generally flat articular surface for Mt III, occupying all except the most volar part of the bone.

The mesocuneiform is a small bone with a slightly concave navicular facet covering most of its proximal side. The slightly convex facet for Mt II oc-
cupies the volar two-thirds of the distal surface. There is also a small articular facet on the tibial side of the mesocuneiform, probably for an entocuneiform. No entocuneiform has been shown for any Moropus species, but apparently a small remnant of the bone was present. It did not articulate with Mt II, and there is no sign of an articulation for it on any naviculars examined. The presence of an entocuneiform in M. elatus, as well as in Ancylotherium (A.) pentelicum where a facet for it is also known on a mesocuneiform specimen (a specimen in the Muséum National d'Histoire Naturelle, Paris, casted as AMNH 10.564), is in disagreement with a statement by Radinsky (1963:7) that the entocuneiform was lost in the Chalicotheriidae. The entocuneiform facet has only a small dorsal to volar extent in M. elatus.
Metatarsals (Figs. 14-15, 17-19, 27).-Metatarsal proportions provide an important means of separating certain Moropus species, for there was apparently an increase over time in width relative to length. Proportions and other morphological features are fairly consistent within a single species, even despite variations in absolute size (Table 6). Thus where intraspecific variation can be evaluated, a metatarsal or other foot element can provide a very useful characterization of a species. For this reason a metatarsal (YPM 13,081, Mt II) was chosen as $M$. elatus lectotype from among the type material mentioned by Marsh (1877). Mammalian feet are often considered too plastic for detailed taxonomic work, but at least in Moropus such a restriction does not seem to apply, possibly because of rapid evolution of and strong selection on the manus and pes while the dentition remained relatively plastic within species and constant between species.

YPM 13,081, the Mt II chosen as the lectotype. corresponds closely in proportions and morphology to specimens from both the Agate Quarries and Morava Ranch Quarry (Fig. 18). There is some variation among Mt II specimens in the size and shape of the concave mesocuneiform facet, which occupies the proximal surface (Fig. 17D). In some (YPM 13,081 and the Morava Ranch Quarry specimens) the facet has a greater dorsal to volar extent and accompanies the ectocuneiform facet to the volar edge, separated from the latter facet by a blunt projection. In others (primarily Agate Quarry specimens) the mesocuneiform facet does not extend so far in the volar direction and is more separated in its volar part from the ectocuneiform facet. The sin-

Table 6.-Length and width (in mm) of metatarsals of selected schizotheriine species, with proportions of width versus length.

| Species and specimens | Greatest length | Greatest distal width | Minimum shaft width | Length/distal width | Length/shaft width |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Mt II |  |  |  |  |  |
| Moropus elatus |  |  |  |  |  |
| AMNH 14,378 ${ }^{\text {a }}$ | 133.7 | 41.6 | 26.6 | 3.2 | 5.0 |
| Moropus elatus |  |  |  |  |  |
| CM 1701 | 109.9 | 30.4 | 18.9 | 3.6 | 5.9 |
| Moropus elatus |  |  |  |  |  |
| YPM 13,081 (lectotype) | 136.2 | 36.4 | 26.2 | 3.7 | 5.2 |
| Moropus elatus |  |  |  |  |  |
| F:AM $54,447^{\text {b }}$ | 137.1 | 38.3 | 24.5 | 3.6 | 5.5 |
| Moropus elatus |  |  |  |  |  |
| (range three Frick specimens ${ }^{\text {b }}$, | 109.3-139.5 | 30.4-37.5 | 20.9-22.3 | 3.4-3.7 | 5.1-6.25 |
| mean three Frick specimens ${ }^{\text {b }}$ ) | 120.0 | 33.6 | 21.6 | 3.6 | 5.5 |
| Schizotherium priscum |  |  |  |  |  |
| Ancylotherium (A.) pentelicum (see specimen in Table 5) | 127.0 | 52.3 | 38.1 | 2.4 | 3.3 |
|  |  | Mt III |  |  |  |
| Moropus elatus |  |  |  |  |  |
| AMNH 14,378 ${ }^{\text {a }}$ | 146.4 | 44.3 | 28.9 | 3.3 | 5.1 |
| Moropus hollandi |  |  |  |  |  |
| FMNH Pl3000 | 130.7 | 39.4 | 28.4 | 3.3 | 4.6 |
| Moropus cf. M. hollandi |  |  |  |  |  |
| F:AM 54,903 | 115.7 | 43.3 | 30.4 | 2.7 | 3.8 |
| Schizotherium priscum |  |  |  |  |  |
| Ancylotherium (A.) pentelicum (see Table 5) | 171.3 | 61.9 | 47.1 | 2.8 | 3.6 |
|  |  | Mt $/ V$ |  |  |  |
| Moropus elatus |  |  |  |  |  |
| AMNH 14,378 ${ }^{\text {a }}$ | 148.3 | 43.9 | 28.2 | 3.4 | 5.3 |
| Moropus elatus |  |  |  |  |  |
| CM 1701 ${ }^{\text {a }}$ | 126.8 | 34.9 | 23.2 | 3.6 | 5.5 |
| Moropus elatus |  |  |  |  |  |
| AM 9955 ${ }^{\text {b }}$ | 158.7 | 51.2 | 36.0 | 3.1 | 4.4 |
| Moropus elatus |  |  |  |  |  |
| (range five Frick specimens ${ }^{\text {b }}$; | 123.9-164.8 | 35.7-45.2 | 26.0-31.9 | 3.5-3.8 | 4.8-5.4 |
| mean five Frick specimens ${ }^{\text {b }}$ ) | 149 | 41 | 29 | 3.6 | 5.1 |
| Moropus cf. M. hollandi |  |  |  |  |  |
| F:AM 54,903 | 129.8 | 38.5 | $27.5^{\text {c }}$ | 3.4 | $4.7^{\text {c }}$ |
| Moropus sp. (St.-Gérand) |  |  |  |  |  |
| Schizotherium priscum |  |  |  |  | 4.7 |
| Ancylotherium (A.) pentelicum (see Table 5) | 147.2 | 59.3 | 45.3 | 2.5 | 3.2 |

${ }^{\text {a }}$ From the Agate Spring Quarries.
${ }^{\mathrm{b}}$ From Morava Ranch Quarry.
${ }^{c}$ Approximate measurement.
gle ectocuneiform facet at the fibular edge of the proximal surface has a primarily fibular, but slightly proximal, orientation (Fig. 18D). In some specimens the area connecting the dorsal and volar parts of this facet is slightly constricted. Distal to the ec-
tocuneiform facet and adjacent to it is a small Mt III facet, whose dorsal and volar parts are connected only by a very narrow band at the facet's proximal edge. A dorsofibular tubercle at the proximal end of all the Mt II specimens helps to prevent


Fig. 18.-Dorsal views of A) left Mt II of F:AM 54.447, M. elatus, from Morava Ranch Quarry, Box Butte Co., Nebraska; B) right Mt II of YPM 13.081, lectotype of M. elatus; C) left Mt 11 of AMNH 14.378, M. elatus, from the Agate Spring Quarries. Sioux Co., Nebraska: D) Fibular view of left Mt II of AMNH 14.378. Facet abbreviations as in Fig. I6.
any dorsal to volar movement of Mt II against the ectocuneiform or Mt III. A depressed area on the fibular surface bordering the Mt III facet is succeeded distally by a strongly rugose area. Very characteristic of this bone is an oblique longitudinal ridge for muscle insertion along the tibiodorsal angle of the proximal part of the shaft; this ridge is more distinct in some specimens than in others. The distal end of Mt II is slightly asymmetrical.

The proximal end of an Mt III of YPM 24.631, a paralectotype of M. elatus (see Fig. 19A, B), is indistinguishable from other referred Mt III specimens but probably belonged to a larger individual than the Mt II considered as the lectotype. On each Mt III specimen, the ectocuneiform facet, on the proximal surface, is rather flat and slanted distally toward the tibial side (Figs. 17D, 19A). The shape of the proximal end of the bone is subtriangular with
the ectocuneiform facet occupying practically all of this surface. On the tibial side of the bone (Figs. 17A, 19A) the small articular surface for Mt III is bipartite with dorsal and volar parts connected by a very narrow strip of articular surface (the connection may be absent in some specimens). Sometimes the dorsal part of the facet is larger, sometimes the volar, and sometimes the parts are subequal. The two facets for Mt IV, on the fibular side of the proximal end (Figs. 17B, 19B), are large compared to the Mt II facet. In some specimens the dorsal and volar facets are distinctly separated by an intervening sharp depression; in others they are directly adjacent though not confluent. In all the specimens examined, the dorsal Mt IV facet is easily the larger (about twice as large as the volar facet), and both facets are flat to slightly concave and slanted slightly toward the center of the fibular


Fig. 19.-Tibial (A) and fibular (B) views of proximal end of Mt III of YPM 24,631, a paralectotype of M. elatus. Dorsal (C) and volar (D) views of rare fused proximal and medial phalanges of digit Il of the pes of M. elatus, F:AM 54.444. from Morava Ranch Quarry, Box Butte Co., Nebraska. Dorsal (E) and volar (F) views of unfused proximal and medial phalanges of digit II of the pes of $M$. elatus, AMNH 14,378, from the Agate Spring Quarries, Sioux County, Nebraska. Facet abbreviations on Mt IIl as in Fig. 16.
surface (probably restricting dorsal to volar movement between Mt III and Mt IV). Distal to the articular surfaces, rugosities are present on the tibial, volar, and fibular surfaces of the shaft. At the distal end of Mt III the phalangeal articulation is roundly convex and laterally symmetrical, separated dorsally by a depression from the shaft of the bone. There are strong lateral tubercles and a prominent but not sharp keel between the sesamoid facets.

In all examined specimens of Mt IV the proximal head is of quadrilateral shape, slightly wider trans-
versely than deep. The proximal surface (Fig. 17D) is occupied almost entirely by the flat to slightly concave cuboid facet, which is separated by the facets on the tibial side of the bone by a sharp dorsal to volar ridge. The proximal end of the tibial surface has two oval-shaped facets for Mt III (Fig. 17C), of which the dorsal is about twice as large as the volar. The two articular platforms are separated from each other by a groove, and the area just distal to the facets is very rugose. Part of the dorsal facet faces in a dorsal as well as a tibial direction. When Mt IV


Fig. 20.-Dorsal (A, C) and ulnar (B, D) views of the duplex of digit II of the manus of a presumed male (A, B) of M. elatus, AMNH 14.427, left side, and presumed female (C, D) of $M$. elatus, AMNH 14.425, right side, both from the Agate Spring Quarries, Sioux Co., Nebraska.
is articulated with Mt III, the contact between the two bones occupies almost all of the volar facet on Mt IV but only the distal three-fourths of the dorsal facet. The remainder of the dorsal facet articulates with the distal fibular edge of the ectocuneiform (Figs. 17C, D). There are no facets on the fibular surface of Mt IV, but the fibular-volar angle of the proximal end is enlarged and appears to overhang the shaft because of some dorsal to volar compression of the shaft's fibular side. The proximal head and distal end of Mt IV are each rotated in a different direction relative to the proximal part of the shaft axis. On the slightly asymmetrical distal end, the tibial lateral tubercle is stronger than the fibular one, and the tibial side of the phalanx articulation extends farther distally.

Pes summary.-Movement in the pes of M. elatus is more restricted than that in the manus, and the pes as a whole is less divergent than the manus from that of other tridactyl perissodactyls. Flexion and extension of the pes occurs primarily at the joint between the tibia and astragalus; most of the joints among tarsals and between tarsals and metatarsals are restricted in size and have stops especially to prevent dorsal to volar fiexion. A small degree of side to side movement is possible, however.

The relatively large number of associated specimens permit the observation that Mt III and Mt IV were subequal in length in M. elatus and that both were longer than Mt II (Table 5). Consistent with this emphasis on both Mt III and Mt IV, the ectocuneiform articulates with Mt IV as well as Mt III so that weight is spread on both digits (the ectocuneiform also has some articulation with Mt II). In Ancylotherium (Ancylotherium) pentelicum (specimen in Muséum National d'Histoire Naturelle, Paris, figured by Gaudry, 1862), Mt III is clearly the longest digit, and there is no contact between the ectocuneiform and Mt IV. Mt IV in $M$. elatus was also capable of some movement in the fibular direction relative to the rest of the pes; during such movement its contact with the ectocuneiform was lost and its ectocuneiform facet then articulated with Mt III. Metatarsals are much shorter than metacarpals of the same animal.

Phalanges of the pes are similar in structure to those of the manus and were presumably capable of roughly the same movements. They are, however, smaller, and there is no special enlargement of the phalanges of digit II of the pes.

## Proximal Phalanges

In M. elatus, morphology of phalanges does not differ markedly from digit to digit, except for the distinctive phalanges belonging to digit II of the manus and pes. Thus an isolated phalanx cannot easily be referred to a particular digit or even to the manus or pes, especially when one considers the great size variation among individuals (Coombs, 1975). Nevertheless, certain generalizations concerning the phalanges are possible.

Digit II manus (Fig. 20).-A large, fused proximal and medial phalanx of digit II of the manus is a characteristic feature of Moropus. Described as a duplex by Holland and Peterson (1914:357-359), such a bone is present, though broken, among the paralectotypes of M. elatus (YPM 24,631, figured
by Holland and Peterson, 1914:223). In juvenile individuals the two bones were not yet fused or were incompletely fused, but in at least one old individual (UCMP 14,377, originally AMNH 14,377, Fig. 21) the ungual phalanx is also fused to the duplex. The angle of fusion in the latter specimen may suggest the usual hooked position of these phalanges during life. Characteristic of the duplex of the manus is the strongly dorsal orientation of the facet for Mc II. The Mc II facet is roughly heart-shaped, without any particular asymmetry, and is gently concave. Its ulnar edge is slightly sharper than its radial one. Two volar tubercles (radial and ulnar), separated by a notch, extend proximally beyond the Mc II facet. The shaft of the duplex is deepest in those specimens where fusion has proceeded most completely; in some specimens the junction of the original two bones has become obscured. Distally the duplex is expanded in the dorsal to volar direction by the curved facet for the ungual phalanx. This facet is shaped like a pulley, with a broad, deep groove between the two flanges, and curves from the dorsal edge of the distal end onto the volar surface of the duplex. Dorsally the groove comes to an end before the disappearance of its lateral flanges so that a stop for dorsal movement of the ungual phalanx is developed. On the volar side, the flanges of the articular facet curve apart and become sharper before they disappear.

When a number of duplexes from digit II of the manus are available, as in the Cook Collection $(\mathrm{N}=9)$ and other collections from the Agate Quarries in the American Museum of Natural History, it becomes clear that two size groups are present. The smaller duplexes (Figs. 20C, D) are slightly less asymmetrical than the larger ones (Figs. 20A, B), and their proximal facet is not quite so flattened at its radial edge. The possibility that such smaller duplexes might belong to a digit other than digit II of the manus must be considered, especially in view of the occasional fusion of phalanges belonging to digit II of the pes. However, the difference in size in this case seems to be due to sex dimorphism, not to phalangeal fusion in additional digits. The mean length of the smaller manus duplexes in the Cook Collection (four specimens) is about $80 \%$ of that of the larger duplexes (six specimens). This ratio corresponds closely to the male/female size ratio calculated from the mean sizes of large and small radii and tibiae given by Coombs (1975). Rare duplexes, which do belong to digit II of the pes (see below), are only about two-thirds the size of the large ma-
nus duplexes and correspond closely to the combined lengths of unfused phalanges of digit II of the pes. Small or intermediate sized duplexes in schizotheriine species other than $M$. elatus must be evaluated carefully to determine whether they belong to the manus or the pes.

Digits III and IV of manus. - In M. elatus much of the great expansion of digit II of the manus is the result of expansion of the ungual phalanx and the part of the duplex representing the medial phalanx. The proximal phalanges of digits III and IV of the manus are not much smaller than the proximal part of the duplex. Because digit III and digit IV proximal phalanges are about the same size, it is difficult to assign each to the correct digit even though they differ from each other in morphology. One kind of proximal phalanx 1) is more symmetrical than the other sort, narrowing rapidly in the distal direction, 2) has metacarpal facets on its dorsal surface but with more proximal orientation than on the duplex, 3) has flattened articular areas on the dorsal surface just distal and adjacent to the metapodial facet (presumably for stops against hyperextension), 4) has some development of variable volar intermediate tubercles on the shaft, increasing the depth of the bone, and 5) has a slightly asymmetrical distal facet (a shallow, curved pulley).

A phalanx of YPM 24,632 (not mentioned by Marsh, 1877, but figured by Holland and Peterson, 1914:224) is among the second sort of proximal phalanx. Features include 1) transversely expanded metacarpal facet, 2) some lateral torsion of the shaft (more than in previous sort), 3) pronounced flattened area on dorsal surface just distal to the metacarpal facet and particularly noticeable on the ulnar (?) side, and 5) distal facet asymmetrical (one side of pulley longer and less curved).

Digit II of pes (Figs. 19C-F).-On a single individual the proximal phalanges of the pes are slightly smaller than those of the manus and are not so strongly expanded at their proximal ends. Digit II of the pes is represented by a comparatively large number of specimens from the Agate Quarries and Morava Ranch Quarry. In all of the specimens the bone is flattened in the dorsal to volar direction compared to most other proximal phalanges, and the articular facet for Mt II has a strongly dorsal orientation (a similarity to the facet for Mc II on the duplex of the manus). The Mt II facet extends onto the proximovolar tubercles, between which there is a pronounced notch. This notch is generally characteristic of the phalanx in its sharp indentation


Fig. 21.-A) Unusual, completely fused proximal, medial, and ungual phalanges of digit II of the manus belonging to UCMP 14,377, M. elatus. B) Radial view of a left ungual phalanx of digit II of the manus of a presumed female of M. elatus, AMNH 14.425. C) Ulnar view of a right ungual phalanx of digit II of the manus of a presumed male of M. elatus, AMNH 14,427. All from the Agate Spring Quarries, Sioux Co., Nebraska. D) Dorsal view of fused proximal and medial phalanges of digit II of the pes of YPM I2,194, type of "M. senex," from Dayville, Oregon.
and small width. A distal facet for the medial phalanx, grooved but with an irregular surface, curves at the distovolar angle of the phalanx. The articulation between proximal and medial phalanges is so close that there could have been little or no movement between them (Figs. 19E, F). Holland and Peterson (1914:375-376) noted the occasional presence among the Carnegie material of fused proximal
and medial phalanges of digit II of the pes. Their observation is borne out by the presence among the Morava Ranch material (F:AM 54444. Figs. 19C, D) of another such example. A duplex for digit II of the pes is best distinguished from that of digit II of the manus by its smaller size and by its articular surface for the ungual phalanx being less deeply grooved and with less strongly flared volar edges.

Such fusion in the pes was quite uncommon in $M$. elatus, probably occurring in no more than one out of ten individuals.

Digits III and IV of pes.-Proximal phalanges of these digits are not easily distinguishable from one another. Both are longer and thicker than unfused proximal phalanges of digit II of the pes. One group of these phalanges (? of digit III) is slightly shorter and more expanded proximally than is the other group. In all of the specimens the articular surface for the metatarsal has more proximal orientation than is on the proximal phalanx of digit II. This difference is consistent with comparisons of digits III and IV of the manus against digit II, except that in the phalanges of the pes flat stopping surfaces at the distal edge of the metatarsal facet are small or absent. This difference probably corresponds to the smaller development on the metatarsals of the tubercles against which the flattened areas of the phalanges may rest during hyperextension. Both phalanges are more symmetrical than their counterparts in the manus.

## Medial Phalanges

Unfused medial phalanges of manus and pes are not easily distinguished in this species. All have a curved concave proximal facet (for the proximal phalanx), divided into two halves by a ridge, and a pulley-like, curved distal facet for the ungual phalanx. Medial phalanges of digits III and/or IV of the manus are more likely than others to have asymmetrical development of the proximal facet. The medial phalanx of digit II of the pes, even where it has not fused to the proximal phalanx, has a right angle bend in its proximal facet which would prevent any movement of the two phalanges against one another.

## Ungual Phalanges (Figs. 21B, C)

Except for the large ungual of digit II of the manus, it is practically impossible to refer ungual phalanges to a given digit, except that in a given individual, unguals of the manus are usually larger than those of the pes.

The large ungual phalanx of digit II of the manus is taller and more transversely compressed than other unguals of this species, and there is a thick, tall dorsal process onto which the duplex facet extends. A large, rugose subungual process prevents the duplex facet from reaching the volar surface of the bone. Although the duplex facet covers a large are at the proximal end of the ungual phalanx, it
does not follow an evenly rounded curve but has a sharp angle between its proximal oriented and volar oriented parts; this angle corresponds to one on the distal facet of the duplex and effectively prevents most movement between the two bones. Dorsally the claws are quite sharp, and there is either equal fission between the dorsal and volar edges of the claws or greater fission dorsally.

An intermediate sized ungual, not so tall nor so strongly compressed transversely as the larger one, belongs to digit III or IV of the manus and has both a large dorsal process and subungual process. As in the larger phalanx, the claws are sharp and cloven equally above and below. The other ungual of the manus compares closely with the unguals of the pes.

Of the three small pes unguals one has a larger dorsal process than the others. Generally the pes unguals are relatively broad transversely, and the two claw sides are separated by a small space. The two sides may be slightly asymmetrical and are usually cloven more deeply above than below. The subungual process is much reduced.

## Sesamoids

A number of sesamoids are known in M. elatus. These articulate with the distovolar surfaces of metacarpals and metatarsals, but it is difficult to determine, which sesamoids go with which digits.

> Moropus distans Marsh
> Moropus distans Marsh, 1877:249.
> Moropus distans: Peterson, 1907b:734; Holland and Peterson, 1914:221; von Koenigswald, 1932:22; Colbert, 1935:13; Belyaeva, 1954:49 (locality incorrectly cited as Nebraska by von Koenigswald, Cobert, and Belyaeva).

## Lectotype

YPM 12,193a, coossified proximal and medial phalanges (duplex) of digit II of pes from the "Bridge Creek beds" in the John Day Basin. Oregon, ?Arikareean (Fig. 22F).

## Paralectotype

Medial phalanx of YPM 24,627 mentioned by Marsh (1877).

## Hypodigm

Cuboid of YPM 24,628, first mentioned and figured by Holland and Peterson (1914:220; see Figs. $16 \mathrm{C}, \mathrm{F}$ ); distal end of Mc II of YPM 24,628 . Paralectotype and hypodigm were collected with the lec-

totype and were originally given the same catalogue number; however, they are probably not the same individual and are renumbered in this paper.

## Diagnosis

A small chalicothere, smaller than any known specimen of $M$. elatus; cuboid having more proximal extension of navicular facet than in M. elatus; duplex of digit II of pes flatter in dorsal to volar direction than rare pes duplexes of $M$. elatus, fusion to form this duplex possibly more common than in M. elatus.

## Discussion

Although Moropus distans is not so well known as M. elatus, Holland and Peterson (1914:217) established it as the type species of Moropus because Marsh (1877) had mentioned it first. Additional material must be obtained before an estimate of the size range in this species can be made. Small average size may be a primitive feature in the genus Moropus (see also Moropus sp. from St.-Gérand-le-Puy, Coombs, 1974). The distribution of M. distans cannot be evaluated without fuller knowledge of other small, early North American chalicotheres, for the species is presently known only from Oregon.

Attention is directed to Moropus oregonensis (Leidy, 1873) from the same region as M. distans. Both species were described before it became known that the teeth and footbones of chalicotheres actually belong to the same kind of animal (Filhol, 1891). M. distans may be synonymous with $M$. oregonensis, which includes only teeth, but conspecificity cannot be established. If evidence of synonymy should become available, M. oregonensis (discussed below) would become the type species of Moropus.

Marsh (1877:250) also named Moropus senex for a duplex, YPM 12, 194 (Fig. 21D), from near Dayville, Oregon. This phalanx, which belongs to digit II of the pes, is described below but has no specific diagnostic features. Moropus senex is therefore considered to be a nomen dubium. The type spec-
imen resembles rare pes duplexes of $M$. elatus but is considered for the present to represent Moropus indet.

## Description and Comments

YPM 12,193a, the small duplex here designated as the lectotype of Moropus distans (Fig. 22F), appears to belong to digit II of the pes but is slightly flatter, especially in the metapodial facet, than duplexes of the same digit in M. elatus and "M. senex." Its distal end is not known, and thus definite identification as a duplex of the pes cannot be made, despite its small size. In addition to its unusually small size compared to other Moropus specimens, this duplex may be significant in the mere presence of fusion of proximal and medial phalanges in a pes digit, for such fusion is rare in M. elatus (no more than $10 \%$ of known specimens). Although it is hazardous to generalize on the basis of limited material, the presence of such a duplex among the very few specimens of $M$. distans may suggest that development of a pes duplex was common in this species. Formation of a duplex for pes digit II is apparently universal in certain Moropus species, for example M. merriami.

Fusion of phalanges to form a duplex of pes digit II is also of interest in the single specimen of " $M$. senex," YPM 12,194 (Fig. 21D). This specimen clearly belongs to digit II of the pes by virtue of its shallow distal facet without flared lateral edges. It is thus not a manus duplex, unless an unusual one, of a small sized Moropus species. Morphological resemblances to an M. elatus duplex of pes digit II from Morava Ranch Quarry (F:AM 54,444, Figs. 19C, D), including a size similarity, make tempting a synonymy of " $M$. senex" with $M$. elatus. YPM 12,194 does not seem to belong to M. distans, but the rarity of phalangeal fusion in the pes of $M$. ela$t u s$ and our lack of knowledge of postcranials of $M$. oregonensis make any taxonomic alignment of " $M$. senex" premature.

YPM 24,627, the medial phalanx paralectotype of M. distans, presents no features of special taxonomic interest, except for small size, nor does the .

## $\leftarrow$

Fig. 22.-A) Holotype of $M$. oregonensis, YPM 10,030 , a right maxillary fragment with $\mathrm{P}^{4}$ and partial $\mathrm{M}^{1}$. B-E) Hypodigm of $M$. oregonensis: left $\mathrm{P}^{3}-\mathrm{P}^{4}(\mathrm{~B})$ and right $\mathrm{M}^{3}(\mathrm{C})$ of YPM $10,030 \mathrm{a}$; left $\mathrm{M}^{1}-\mathrm{M}^{2}(\mathrm{D})$ of YPM $10,030 \mathrm{~b}$; and right $\mathrm{M}^{3}$ ( E ) of AMNH 7259. F) Lectotype of $M$. distans, YPM 12,193a, coossified proximal and medial phalanges of digit II of the pes. A-D and F are from the "Bridge Creek Beds" in the John Day Basin, Oregon; E is from "near Antelope Springs," Oregon. G and H) Dorsal (G) and volar (H) views of a left carpus of M. hollandi, FMNH P13000 (minus pisiform), from near Jay Em, Goshen Co., Wyoming. Bones correspond to those of right carpus of M. elatus labeled in Fig. 9; facet abbreviations as given in Fig. 10.

Mc II distal end of YPM 24,628. Both specimens generally resemble their counterparts in M. clatus except that the two sesamoid facets on the $M$. distans Mc II are slightly less unequal in size than they are in $M$. clatus.

The cuboid of YPM 24,628 is small, with a maximum dorsal to volar thickness of 47 mm , compared with 75 mm for AMNH 14,378 (a medium-sized cuboid of $M$. elatus). Morphologically, the specimen is close to cuboids of M. elatus, M. hollandi, and M. merriami, but the tibiovolar rugose process is proportionately somewhat smaller than in other Moropus specimens (Figs. 16C, F). Unfortunately the volar part of the tibial side of the bone is damaged, so that the extent of navicular and ectocuneiform facets are not completely clear. Nevertheless, the navicular facet appears to extend proximally to reach the proximal edge of the tibial side and thus adjoins the facet for the calcaneum (Fig. 16C). Such proximal extension of the navicular facet is seen in M. merriami (UCMP 78,727) but not in M. elatus or M. hollandi. The ectocuneiform facet on the $M$. distans cuboid, though broken at its volar edge, is apparently single rather than double; $M$. clatus has variably a single or double facet, but more typically a double one.

## Moropus oregonensis (Leidy)

Lophiodon oregonensis Leidy, 1873, pl. 2, fig. 1 (also described without name pp. 219-220).
Lophiodon oregonensis: Sinclair, 1901:702.
Moropus oregonensis: Holland and Peterson, 1914:219; Colbert. 1935:13; Belyaeva 1954:49.

## Holotype

YPM 10,030 , right maxillary fragment with worn $\mathrm{P}^{4}$ and partial $\mathrm{M}^{1}$ from Bridge Creek area, John Day Basin, Oregon (specimen label states "upper John Day beds"): ?Arikareean; see Fig. 22A.

## Hypodigm

Left $\mathrm{P}^{3}-\mathrm{P}^{4}$ and right $\mathrm{M}^{3}$ of YPM 10,030a, which may be part of the same individual as the type but were not figured by Leidy (Figs. 22B, C); YPM $10,030 \mathrm{~b}$, left $\mathrm{M}^{1}-\mathrm{M}^{2}$ collected at the same locality as type (Fig. 22D); AMNH 7259, M ${ }^{3}$ (Fig. 22E) from "near Antelope Springs, Oregon."

## Diagnosis

Species known only from dental remains, smaller than the smallest known representatives of M. clatus; metaloph on unworn upper molars (especially
$\mathrm{M}^{3}$ ) with labial origin very close to mesostyle, even closer than in M. elatus; upper molars not strongly elongated; $\mathrm{P}^{3}$ and $\mathrm{P}^{4}$ without strong anterolingual or posterolingual cingula and with wear along transverse lophs proceeding to protocone before lophs are completely worn away (especially along metaloph).

## Discussion

Like Moropus distans, Moropus oregonensis shows a number of similarities to Moropus merria$m i$ and some of its undescribed Hemingfordian relatives, possibly more resemblance than to Moropus elatus. Although of small size, the known teeth of M. oregonensis are slightly larger than might be expected to belong to the same individuals as the small postcranials of M. distans. Nevertheless these two species may be synonymous, for the possibility of sexually dimorphic size differences must be considered. The labial origin of the metaloph so close to the mesostyle on unworn $\mathrm{M}^{3}$ is a character shared with Sclizotlocrium (see $S$. priscum in Coombs, 1976); it is apparently primitive within the genus Moropus and is lessened in more advanced species.

## Description and Comments

$M^{3}$ (Figs. 22C, E).-The two available specimens, YPM 10,030a and AMNH 7259, are of similar size. At a glance they appear to have quite different morphology, but most of the points of variance are easily explained by wear, for AMNH 7259 had only recently erupted. In the unworn tooth the origin of the metaloph is very close to the mesostyle, whereas in the worn tooth the origin has moved posterolingually. All parts of the metaloph are of approximately equal height, but there is a slightly separated summit, representing the hypocone, at the lingual end of the metaloph. The anterior part of the tooth, including the relatively large protoconule and complete protoloph, is little worn even on the more worn specimen, YPM 10,030a. In neither specimen does a branch of the anterolingual cingulum join the protoloph to ascend to the tip of the protocone. In YPM 10,030a, the anterolingual cingulum remains separate, ridge-like and uniform as it skirts the protocone lingually; posteriorly it enters the central valley as a weak ridge or fold but does not close off the lingual opening of the central valley. In AMNH 7259 the cingulum is less uniform and approaches the wall of the protocone more closely but does not fuse with it. The postfossette
is partly closed off by the posterior cingulum, and a labial rib is present opposite the paracone. On AMNH 7259 a very small crista (see Butler, 1965:178, for definition) is present. Principal differences from M. elatus include the smaller degree of wear on the protoloph and the morphology of the anterolingual cingulum. The origin of the metaloph is closer to the mesostyle in an unworn specimen than in any other known Moropus species, even $M$. elatus.
$M^{2}$ and $M^{1}$ (Fig. 22D).—In addition to its smaller size, $\mathrm{M}^{1}$ is more quadrate (less elongated compared to width) than $\mathrm{M}^{2}$. Both teeth closely resemble $\mathrm{M}^{3}$. but on $\mathrm{M}^{2}$ a branch of the anterolingual cingulum appears to join the protoloph (but weakly), in contrast to $\mathrm{M}^{3}$. The parastyle and mesostyle, particularly on $\mathrm{M}^{2}$, are slightly weaker than they are in $M$. elatus. Posterior to the protocone the lingual cingulum is only weakly visible.
$P^{3}$ and $P^{4}$ (Figs. 22A, B).-Known upper premolars are somewhat worn. They show many similarities to specimens of M. elatus, but in their pattern of wear come closer to some of the small Hemingfordian relatives of M. merriami. It is clear, despite wear, that the two transverse lophs were complete and that a protoconule was present. Wear reaches the protocone earlier in the life of each tooth than it does in $\mathrm{P}^{3}$ and $\mathrm{P}^{4}$ of $M$. elatus, for in these specimens the protocone has been worn nearly flat and lies quite below the level of the protoloph at the same time that the protoloph is still completely or at least partially visible. Apparently wear proceeds from the ectoloph along the metaloph to the tip of the protocone fairly early during the life of the animal, whereas wear along the protoloph is much slower. Wear on the anterior part of the ectoloph slightly reduces the parastyle in comparison to that often seen in even more worn specimens of M. elatus. Anterolingual and posterolingual cingula are not at all expanded but form a uniform ridge skirting the protocone, fusing with it at only one point.

## Moropus hollandi Peterson

Moropus elatus: Peterson, 1907a:60.
Moropus hollandi Peterson, 1913:673.
Moropus hollandi: Holland and Peterson, 1914:232.
Moropus elatus: Matthew, 1929:520.
Moropis hollandi: von Koenigswald, 1932:22; Colbert, 1935:13; Belyaeva, 1954:49.

## Holotype

CM 1424, a partial skeleton of a medium-sized individual, including radius-ulna, scaphoid, trape-
zoid, magnum, unciform, Mc II-V, femur, two tibiae, two astragali, two calcanea, duplex of digit II of manus, proximal phalanx, and medial phalanx. from Peterson’s (1907a) Upper Harrison beds near Nebraska-Wyoming state line along Niobrara River. Early Hemingfordian. Many of the elements of the holotype of $M$. hollandi were figured by Holland and Peterson (1914) and, except for the scaphoid and trapezoid (Figs. 26E-H), are not repeated in the present paper.

## Hypodigm

F:AM 54902a-1, two scaphoids (Fig. 26C), two lunates (Fig. 26D), distal end of radius, distal end of radius-ulna, cervical vertebra VII, two proximal phalanges, astragalus (Fig. 23C), sesamoid, proximal end of ulna, and cuboid, from Upper Harrison equivalent beds (Skinner, 1968) 7 mi south of Chugwater, Wyoming; FMNH P13000, an atlas (Fig. 6 B), pelvis, almost complete left manus (Figs. 22G, H, 24, 25, 26A, B), duplex and ungual phalanx of digit II of manus (Figs. 28D-F), and navicular, cuboid, and Mt III of left pes (Figs. 16A, D, G, 27B, D-F) from "Jay Em Creek, 2 mi east of ranch, Lusk, Wyoming;'" and FMNH P12094, a skull (Figs. 23A, B) from the "east wall of Jay Em Creek, a tributary of Rawhide Creek, near Lusk, Wyoming." The Field Museum specimens, collected by Riggs near Jay Em, probably also come from Upper Harrison equivalent beds. All the material referred to F:AM 54.902 is larger than the holotype, and some of it probably belongs to a single individual.

## Additional Material

F:AM 54,903, a Mt III and Mt IV from Upper Harrison equivalent beds (Skinner, 1968) near Jay Em, Wyoming, is here referred to Moropus of. M. hollandi. Its uncertain reference is because of differences, whose significance is unclear, between its Mt III (Figs. 27C, 28A-C) and that of FMNH PI3000. The latter specimen is more definitely referable to $M$. hollandi by virtue of its known manus morphology.

## Diagnosis

Moropus species resembling M. elatus in most respects, including size, dental morphology, and absence of proximal extension of navicular facet on the cuboid. Differs from M. elatus in the generally shorter proportions of Mt III relative to minimum shaft width (Table 6) and from all known Moropus species in the absence or strong reduction of a tra-
pezium in the manus. Trapezium facets absent on scaphoid, Mc II, and probably on trapezoid. Lunate, cuneiform, and trapezoid commonly compressed in the dorsal to volar direction relative to their width.

## Discussion

The Frick and Field Museum specimens cited in the hypodigm are of great importance in affirming M. hollandi as a separate species. Three additional scaphoids, one trapezoid, and one Mc II, all of which closely resemble the holotype, and new metatarsal specimens reinforce the idea that the differences of the holotype of $M$. hollandi from $M$. elatus are not mere individual peculiarities. Absence of a trapezium, along with the dorsal to volar compression of several carpals, suggests a degree of superflexion of the manus unusual within Moropus.

The large number of similarities between $M$. hollandi and $M$. elatns emphasize the close affinities between these two species. At the same time they create difficulties in identifying specimens, especially in those many cases where diagnostic elements of M. hollandi are not included. Because of difficulties in identification, it is still unclear whether the two species are separated by a temporal boundary or whether their occurrences reflect ecological differences in the assemblages in which they are represented. Additional specimens may someday show a morphological continuity in the evolution of M. hollandi from a population of M. elatus. Certainly some aspects of M. elatus morphology, when taken at one end of their range of variation (for example, shorter proportions of some metatarsals) approach conditions seen in M. hollandi. On the other hand, no M. elatus specimen shows the scaphoid, trapezoid, or Mc II characteristics considered diagnostic of $M$. hollandi.

Absence of a trapezium occurs in Moropns, so far as is known, only in M. hollandi. It is paralleled, however, in Ancylotherium (Ancylotherium) pentelicum, where there is an even greater degree of mobility of the scaphoid on the trapezoid. There the scaphoid contacts Mc II during extreme flexion as was reported by Schaub (1943; although Schaub concluded, probably erroneously, that the trapezium in Ancylotherium was fused with Mc II). Schizotherium turgaicum and Borissiakia betpakdalensis apparently have also independently lost the trapezium (see Borissiak, 1946; Belyaeva, 1954).

Slight proportionate shortening of the metatarsals
of M. hollandi compared to M. elatus is consistent with the gradual shortening over time of metatarsals among a number of schizotheriine species (see Coombs, 1974). The Mt IV proportions of F:AM 54,903 (Moropus cf. M. hollandi) most closely approach those of the small Mt IV of Moropus sp. from Aquitanian deposits of St.-Gérand-le-Puy, Allier, France (Table 6).

Present evidence suggests that $M$. hollandi had a size range rather similar to that of $M$. elatus. The two best preserved individuals (the holotype and FMNH P13000) are of modest size, however, but material in F:AM 54,902 suggests that larger individuals were also included in the species. The holotype and FMNH P13000 probably represent females, and the morphology of their duplex phalanges of the manus also supports this conclusion (see discussion of M. elatus duplexes).

## Description and Comments Skull and Upper Dentition (FMNH P12094, Figs. 23A, B)

The single skull with upper teeth known for $M$. hollandi falls within the range of morphology of $M$. elatus and shows no special differentiating features. There is no sign of doming or skull elaboration, and certain landmarks, like the internal nares and infraorbital foramen, are in the same position as they are in M. elaths. The upper teeth also cannot be differentiated from those of M. elatus, although the length of the toothrow ( $\mathrm{P}^{2}-\mathrm{M}^{3}$ ) falls near the lower end of the $M$. elatus size range and the premolar row may be proportionately shorter. The teeth in this specimen are very little worn, so that the protoconule and protoloph on $\mathrm{M}^{3}$ are still complete. The labial origin of the metaloph on $\mathrm{M}^{3}$ is still quite close to (less than 10 mm from) the lingual base of the mesostyle. The base of the protocone is not folded in the central valley. Premolars of FMNH P12094 are most similar to those specimens of $M$. elatus in which the protoloph of $\mathrm{P}^{2}$ is not strongly developed and the lingual cingula of $\mathrm{P}^{3}$ and $\mathrm{P}^{4}$ are relatively small. On $\mathrm{P}^{3}$ and $\mathrm{P}^{4}$ the protoloph is taller than the metaloph, which is more worn. Despite the progressing wear on protoloph and especially metaloph, the protocone is still completely unworn, a similarity in wear pattern to M. elatus as compared to M. oregonensis .

## Vertebrae and Pehis

The atlas and pelvis (FMNH P13000) cannot be easily differentiated from specimens of M. elatus.


Fig. 23.-Lateral view of skull (A) and occlusal view of right $\mathrm{P}^{2}-\mathrm{M}^{3}$ (B) of $M$. hollandi. FMNH P12,094, from near Jay Em, Goshen Co., Wyoming. Volar view of astragalus (C) of F:AM $54,902 \mathrm{~g}$, referred to M. hollandi, from 7 mi south of Chugwater, Wyoming. For facet abbreviations on astragalus see Fig. 14.

However, the proportions of the atlas are slightly different (see Fig. 6), for the anterior to posterior length of the ventral arch is small relative to the transverse width of the articular surfaces for the occipital condyles. F:AM $54,902 \mathrm{e}$, a cervical vertebra VII, corresponds generally with specimens of M. elatus but is also rather broad, particularly anteriorly.

## Forelimb

CM 1424, the holotype of M. hollandi, includes much of one forefoot; additional forelimb material belonging to F:AM 54,902 and FMNH P13000 makes the forefoot the best known part of the skeleton of M. hollandi. The fused radius-ulna of CM 1424 does not differ from specimens of M. elatus in
any important way but is strongly fused into a single unit for more of its length than are most $M$. elatus specimens. There is a slight difference between F:AM 54,902c and F:AM 54,902d, both of which include the distal ends of radii, in that the former has a more strongly compressed and dorsal to volar concave distal facet for the lunate. The less compressed condition (F:AM 54,902d) is more similar to that in M. elatus, but the compressed condition corresponds more closely to the morphology of the lunate of F:AM 54902b (Fig. 26).

The carpus provides the principal characters by which M. hollandi is distinguished from M. elatus. The scaphoid differs from that of $M$. elatus in the apparent lack (or at least very strong reduction) of a trapezium facet, so prominent on the radiovolar


Fig. 24.-Proximal (A. C, radial edge at left) and distal (B, D, radial edge at right) views of left scaphoid, lunate, and cuneiform (A, B) and left trapezoid, magnum, and unciform (C, D) of M. hollandi, FMNH P13000, from near Jay Em, Goshen Co., Wyoming. Facet abbreviations as in Fig. 10.
surface of the scaphoid in other Moropus species. In $M$. hollandi, the same area is occupied by a ridge separating the rough radiovolar surface from the smooth saddle-shaped trapezoid facet distal to it (Figs. 22H, 26A, C, E). The trapezoid facet (Fig. 24B) is very similar to its counterpart in M. elatus, as is the proximal lunate facet (Figs. 26B, F). The distal lunate facet is also similar but does not extend so far in the proximal and volar directions; however, it does reach the edge of the trapezoid facet in its most proximal part. As in M. elatus, the distal process is squared with a relatively flat magnum facet on its distal surface, bordered by trapezoid and distal lunate facets (Fig. 24B).

Two lunate specimens are slightly compressed in the dorsal to volar direction, with proximal and dis-
tal scaphoid facets curtailed at their volar edges (Fig. 25A). In F:AM 54,902b (Fig. 26D) the volar process is also rather short, and the facet for the radius is very strongly convex in a dorsal to volar direction and abbreviated at its volar edge. A third, larger, specimen (F:AM $54,902 \mathrm{k}$ ) has a large volar process and does not seem to be compressed.

The single cuneiform specimen, like the lunate of the same individual (FMNH P13000), shows a tendency toward compression in a dorsal to volar direction. Such abbreviation on the cuneiform is mostly in the lunate (Fig. 25C) and unciform (Fig. 24B) facets; the unciform facet is more concave than in specimens of M. elatus and is set off by a volar ridge.

The unciform (two specimens) is basically similar


Fig. 25.-A) Radial view of left lunate, magnum, and Mc III (dorsal edge at right), B) ulnar view of left lunate, magnum, and Mc III (dorsal edge at left), C) radial view of left cuneiform, unciform, and Mc IV (dorsal edge at left), and D) proximal view of left Mc II, Mc III, and Mc IV (dorsal edge below, radial at left) of M. hollandi, FMNH PI3000, from near Jay Em, Goshen Co., Wyoming. Facet abbreviations as in Fig. 10.
to that of M. elatus. On the radial surface (Fig. 25 C ), the platformed magnum facet extends farther distally, however, and is separated from the Mc III facet by a clearly defined ridge. Distinctness and slant of the magnum facet of these specimens resembles those in Morava Ranch Quarry specimens of M. elatus slightly more than those from Agate. At its proximal edge the magnum facet has a narrow proximal strip of facet passing in a volar direction from the main body of the facet and bordering the radial edge of the lunate facet for some distance; this addition to the magnum facet is present in some but not all $M$. elatus specimens and presumably allows tighter articulation between magnum and unciform. As in M. elatus, the boundary between Mc III and Mc IV facets is indistinct. Because of the
great distal extent of the magnum facet, that for Mc III is a bit smaller than the one in M. elatus; there appears to be another tiny area of contact with Mc III, only rarely present in M. elatus, on the radial side of the ulno-volar process.

The two known magnum specimens resemble material of M. elatus very closely, except that the more distal extension of the contact between magnum and unciform is reflected in a flat and rather inconspicuous distal continuation of the unciform facet on the magnum (Fig. 25D).

The trapezoid differs from that of $M$. elatus in several points, the most important being the absence of a trapezium facet. The scaphoid facet of CM 1424 (Fig. 26G), like that of M. elatus, curves onto the radiovolar surface of the trapezoid, but


Fig. 26.-A) Radiovolar view of left scaphoid, trapezoid, and Mc II, and B) ulnar view (dorsal edge at left) of left scaphoid, trapezoid, and Mc II of M. hollandi, FMNH P13000, from near Jay Em, Goshen Co.. Wyoming. C) Radiovolar view of left scaphoid of $M$. hollandi, F: AM 54.902a, and D) proximal view (volar edge below) of right lunate of M. hollandi, F: AM $54,902 \mathrm{~b}$, both from 7 mi south of Chugwater, Wyoming. E) Radiovolar, and F) ulnar views of left scaphoid, and G) radiovolar, and H) ulnar views of left trapezoid of holotype of $M$. hollandi, CM 1424, from near the Wyoming state line along the Niobrara River, Sioux Co., Nebraska. Facet abbreviations as in Fig. 10.
instead of merging with a facet for a trapezium, it passes distally for almost the height of the trapezoid. It does not, however, quite adjoin the Mc II facet at the distal end of the trapezoid but is shaped like a tongue with its volar and distal edges especially well defined. When the scaphoid is moved along the trapezoid, its concave distal surface follows the contour of this facet all the way to the distal edge of the trapezoid. This range of movement suggests that the entire radiovolar facet was indeed for the scaphoid. The scaphoid facet in FMNH P13000 (Fig. 26A), although resembling that in $M$. elatus in not being clearly abbreviated at its
distal edge, was probably also only for the scaphoid. Scaphoid and Mc II in this specimen show no trace of trapezium facets, and the scaphoid during extreme flexion of the carpus reaches close to the trapezoid's distal edge. It is probable, considering the absence of trapezium facets on scaphoid, trapezoid, and Mc II, that no trapezium was present in M. hollandi. This possibility was mentioned by Holland and Peterson (1914:233), but their evidence for it was not so strong, for they thought that a trapezium facet was present on the trapezoid. Trapezoids of $M$. hollandi also are more abbreviated at their volar edges than are those of $M$. elatus.

Mc II (two specimens) shows basic similarity in articular facets to Mc II of M. elatus, including the following: 1) the concave nature of the trapezoid facet, which is set off by well-defined ridges from all other facets (Fig. 25D); 2) the lack of strong proximal orientation of the volar part of the magnum facet and of any sharp ridge separating it from the trapezoid facet (Fig. 25D); 3) Mc III facet overhung for almost all of its extent by the magnum facet (Fig. 26B). These features are not shared by certain other North American schizotheriine species. The radiovolar angle of the proximal end of Mc II differs from all known Moropus species in the absence of a trapezium facet and the weakly developed radiovolar process (Fig. 25D). There is no difference from $M$. elatus in the shaft or distal end.

The proximal end of Mc III is narrower in relation to its depth than in other Moropus species, and this narrowness is reflected in the shape of the proximal facets. The proximal part of the Mc II facet is flatter than that in M. elatus and slants more dorsally (Fig. 25A); as in M. elatus it is continuous with the dorsal part of the Mc II facet. Magnum and unciform facets (Fig. 25D) are both narrower than, but otherwise similar to, the same facets in M. elatus. On the ulnar side of Mc III, weakly overhung by the unciform facet, are two Mc IV facets in the holotype, the dorsal facet larger and separated from the volar one by a depression of greater width than any seen on specimens of $M$. elatus. However, the joining of these two facets in FMNH P13000 (Fig. 25B) suggests that variability of the Mc IV facet(s) persisted in M. hollandi. Shaft and distal end of Mc IV are similar to those in M. elatus.

Mc IV is quite similar to its counterpart in $M$. elatus. There are two separate articular facets for Mc III (Fig. 25C); the dorsal facet differs in the holotype from that in M. elatus in being not much larger than the volar facet, in being concave, and in having an orientation far more radial than proximal. These unusual features are not shared, however, by FMNH P13000. An important feature of the ulnovolar surface of Mc IV is the weaker development than in M. elatus of ulnar and volar tubercles (Fig. 22H). There is, however, the same depression between the tubercles that occurs in $M$. elatus, and an Mc V facet is clearly developed and separated by a space from the proximal edge of the bone.

Only the proximal end of Mc V is preserved in CM 1424. The preserved part has a single cup-
shaped facet for Mc IV on its dorsoradial side. Distally the bone does not seem to diverge as far from Mc IV as does Mc V of M. elatus.

## Hindlimb

A left femur and two damaged tibiae are preserved in the holotype, but these cannot be differentiated from specimens of M. elatus.
The holotype also preserves both astragali, and F:AM $54,902 \mathrm{~g}$ (Fig. 23C) represents an additional specimen. In each, there is a distinct, short distal neck, similar to that in M. elatus. In dorsal aspect the three bones are similar to one another and to $M$. elatus in 1) the greater transverse width of the fibular side of the trochlea and its more gradual slope compared with the tibial side, 2) the somewhat greater proximal extension of the tibial side, and 3) the distal extension of the free part of the fibular side to the level of the distal articular facet. In the holotype the relief on the volar surface of the astragalus is considerably less than in F:AM 54,902g and in M. elatus. Its ectal facet is quite shallowly and uniformly concave, and the strong ridge separating the ectal facet proximally from the trochlea is straight (as in $M$. elatus) rather than curved. There is barely any eminence between the confluent ectal and calcaneal facets, and the sustentacular facet, weakly convex, is abruptly truncated at its almost straight proximofibular edge. Between the sustentacular and ectal facets is a broad but relatively shallow depression. In F:AM $54,902 \mathrm{~g}$ the volar facets, while resembling in shape those of the holotype, have a very strong relief. The large ectal facet is especially deep in its distal part and is divided from the also slanted, contiguous calcaneal facet by a very sharp ridge. A deep but narrow groove separates the ectal from the sustentacular facet. A difference from both the holotype and $M$. elatus is the curved rather than straight proximal crest between the ectal facet and trochlea. All three astragali have a navicular facet on the distal surface very similar to that in M. elatus. In astragalus proportions there is a distinct dichotomy between $M$. elatus and M. hollandi on the one hand and all known later North American specimens (and also later Eurasian schizotheriines) on the other. $M$. elatus and $M$. hollandi are similar in that the proportion of tibial height/transverse width in all specimens (Table 4) falls between 0.72 and 0.81 ; in contrast, the later North American specimens have a lower value (range $0.61-0.66$ for a total of four specimens). The decrease in the ratio in the later spec-


Fig. 27.-Dorsal views of A) right Mt III of M. elatus, AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska, B) left Mt 111 of M. hollandi, FMNH P13000, from near Jay Em, Goshen Co., Wyoming, and C) left Mt III of Moropus cf. M. hollandi, F:AM 54.903 , from near Jay Em, Goshen Co.. Wyoming. Proximal (D. dorsal edge below), tibial (E), and volar (F) views of Mt III of M. hollandi, FMNH P13000. Facet abbreviations as in Fig. 16; X = broken surface: unlabeled line to Mt IV facet.
imens is related not only to genuine broadening of the bones relative to height but also to reductions in the neck (particularly in Moropus merriami) and a decrease in height of the tibial side of the trochlea relative to the fibular side.

On the two broken calcanea of the holotype the tuber calcis is relatively shorter than in M. elatus, and there is only a slight volar prominence at the end of the tuber. As might be expected from holotype astragali (above), the ectal facet is not so
strongly convex as in M. elatus and apparently does not extend so far onto the tuber. No facet for the tibia can be discerned in this individual. The sustentacular process is broken off, but the well-developed "lesser process" remains, separated by a sharp ridge from the cuboid facet on the distal surface. This latter facet is pear-shaped as in M. elatus but almost completely flat.

Two known cuboids resemble specimens of $M$. elatus and differ from $M$. distans and $M$. merriami


Fig. 28.-Tibial (A) and fibular (B) views of Mt III and proximal view (C) of Mt III and Mt IV (dorsal edge below) of F:AM 54,903, Moropus cf. M. hollandi. Dorsal (D) and ulnar (E) views of left duplex, and ungual phalanx (F) of digit II of the manus of FMNH P13000, a presumed female specimen of M. hollandi. All specimens from near Jay Em, Goshen Co., Wyoming. Facet abbreviations as in Fig. 16.
in the failure of the navicular facet to reach the proximal edge of the bone or to adjoin the calcaneum facet (Fig. 16A). Navicular and cuboid are thus separated at their proximal and volar edges by a small space. In this specimen dorsal and volar parts of the ectocuneiform facet are continuous and show no constriction between them, whereas in $M$. elatus the two parts of the facet are sometimes separate. The dorsal part of the ectocuneiform facet
extends distally to adjoin the Mt IV facet, but the volar part of the facet is well separated from the distal end of the cuboid. In this individual the tibiovolar process is not remarkably developed (Fig. 16A). A navicular of FMNH PI3000 (Fig. 16G) falls easily within the range of morphology of M. elatus and cannot be differentiated in any special way.
No metatarsals are known from the type of $M$. hollandi, but FMNH P13000 preserves a Mt III
(Figs. 27B, D-F), which can be compared with Mt III and Mt IV of F:AM 54,903 (Moropus cf. M. hollahdi, see Figs. 27C, 28A-C). Table 6 gives the length versus width proportions of metatarsals of M. hollandi and M. elatus. FMNH P13000 (Mt III) falls within the range of $M$. elatus in length/maximum distal width but has a lower length/minimum shaft width than most specimens of M. elatus. Apparently, broadening of the metatarsal shaft relative to length has proceeded in M. loollandi despite continued resemblance to $M$. elatus in many other respects. Mt III and Mt IV of F:AM 54,903 fall below the range of M. elatus in both proportions. Mt III of FMNH P13000 and F:AM 54,903 complement one another in preservation in that the proximal end of the former is broken at the dorsofibular angle, whereas that of the latter lacks the facets for Mt II and most of the volar part of the facet for Mt IV. The subtriangular, tibially slanted proximal facet, for the ectocuneiform (Fig. 27D), resembles its counterpart in M. elatus, as does the small bipartite Mt II facet (Fig. 27 E ), where it is preserved in FMNH P13000. In this specimen dorsal and volar parts of the Mt II facet are connected by a thin proximal articular platform. Facets for Mt IV differ between the two Mt III specimens. In FMNH P13000 the shape of the volar part of the facet suggests that it was discrete and well separated from the dorsal Mt IV facet (Fig. 27F). In F:AM 54,903 the two parts of the Mt IV facet are not only adjacent but are confluent at their most proximal edges (Fig. 28B). Further, the two parts of the facet in this latter specimen are more closely equal in size than in M. clatus: the situation in FMNH P13000 is not clear. Both specimens show more dorsal to volar compression of the shaft, especially toward the distal end, than occurs in M. elatus. This change seems to be concomitant with the shortening and broadening of the shaft.
Mt IV of F:AM 54.903 is slenderer and distinctly longer than Mt III of the same specimen, proportionately more so than in M. elatus. The greatest difference between this bone and specimens of $M$. elatus is the presence of one continuous facet rather than two facets on the tibial side of the proximal end, corresponding with facets on Mt III above. The two parts of the facet are of almost equal size (the dorsal part is slightly larger), and the connection between them begins at the crest dividing them from the cuboid facet and continues distally over half of the facet. In addition to this partial dorsalvolar division, there is a functional division into
proximal and distal parts, separated only by a barely visible ridge. The more proximal part of the facet, with a proximal to tibial orientation, articulates with the ectocuneiform (Fig. 28C), while the larger, more distal parts of the facet articulate with Mt III. There is strong development of the fibulovolar angle of the proximal end of this Mt IV, although not so strong as in M. elatus, and there is a weak longitudinal ridge on the fibular side of the shaft. The distal end of this specimen is clearly asymmetrical.

## Phalanges

A single large duplex of digit II of the manus belonging to the holotype and two similar duplexes of FMNH P13000 (Figs. 28D, E) suggest by their size and morphology that both of these specimens are females, a conclusion consistent with the small size of these individuals compared to known males of M. elatus. The specimens are quite similar to those of female M. elatus in having a less flattened, more symmetrical Mc II facet than in M. elatus males. These duplexes are compressed transversely but thickened in the dorsal to volar direction, more so than is usual in M. elatus.

Additional proximal phalanges are available but add little to characterization of $M$. hollandi. Most of these appear to belong to digits III or IV of the manus, but one specimen, belonging to F : AM 54.902 f , may belong to digit III or IV of the pes despite its unexpectedly large size. This specimen has a pronounced thickening of its volar part, remarkable because in this and other features it is extremely similar to F:AM 54,911 from Flint Hill Quarry in the Batesland Formation of South Dakota. The presence of M. hollardi in the early Hemingfordian fauna of the Batesland Formation is unclear, however, for other Moropus material from Flint Hill Quarry collected by the University of California shows no special resemblance to known specimens of M. hollardi. M. hollandi is not known from the roughly contemporaneous fauna of the Runningwater Formation of Nebraska.

Small medial and ungual phalanges of $M$. hollandi show no features of particular taxonomic interest. A large ungual phalanx belonging to FMNH P13000 (Fig. 28F) closely resembles the large ungual phalanx of digit II of the manus in M. elatus but is slenderer. Its dorsal and subungual processes are large, but the facet for the duplex is not deeply excavated and has only a weak keel dividing its two halves.

## CONCLUSIONS AND ZOOGEOGRAPHY

The genus Moropus is derived relative to Schizotherium in its higher crowned and more elongated molar teeth, in the absence of a hypoconulid on $\mathrm{M}_{3}$, in the proportionate shortening of metatarsals, and in fusion of proximal and medial phalanges of digit II of the manus to form a duplex bone. Its closest relatives among the Schizotheriinae are Phyllotillon, Ancylotheriun, and a yet unpublished genus of North American Miocene schizotheriine. These genera share the above characters with Moropus, but they are additionally derived in a number of others, for example, the presence in Ancylotherinm and sometimes in Phyllotillon of a crochet and posterior labial rib on upper molars.

The four Moropus species discussed in this paper are all relatively primitive representatives of Moropus, little removed from the Eurasian/North American common stock of the genus (see Coombs, 1974). M. distans, the type species, is poorly known but includes Moropas individuals of relatively small size. Because the few available remains of M. distans include a duplex of digit Il of the pes, it is possible that phalangeal fusion to form a pes duplex was more common in M. distans than in M. elatns. M. distans also differs from M. elatus but resembles Moropus merriami in the more proximal extent of its navicular facet on the cuboid. Moropus oregonensis is known only from upper premolars and molars, which are smaller than comparable teeth of M. elatus and differ in the manner of wear on upper premolars. M. distans may be synonymous with $M$. oregonensis, but no elements clearly linking the two species have yet been found. Moropas senex, known from a single specimen, shows no useful features for differentiating species and is therefore considered a nomen dubium.

Moropus elatns is the best known Moropns species and is the most useful basis for intrageneric and intergeneric comparisons. Male M. elatus are at the extreme high end of Moropus size range, and the molar teeth of M. elatns are slightly more elongated and high crowned than those of $M$. oregonensis. Yet M. elatus has otherwise diverged little from its common ancestry with $M$. distans and $M$. oregonensis. Moropus hollandi ciosely resembles M. elatus but differs in the loss or strong reduction of the trapezium in the manus and the dorsal to volar compression of certain other carpal elements. Loss of the trapezium occurs independently in Schizotheriun turgaicum, Borissiakia betpakdalen-
sis and Ancylotherinm (Ancylotherinm) pentelicum but within Moropus is characteristic only of M. hollandi, where it presumably allowed increased flexion of the carpus. M. hollandi also has proportionately shortened its metatarsals relative to most of $M$. elatus, consistent with a general trend toward such shortening within the Schizotheriinae over time. On the basis of the above given similarities and differences, Moropus clatus and M. hollandi seem to be closely related, whereas $M$. distans and M. oregoneusis may be closer to M. merriami. Moropus merriani and its kin will be more thoroughly discussed in a separate paper, as will Moropus matthewi.

It is difficult to discuss the zoogeography of early Moropus species on present scanty evidence. M. distans and $M$. oregonensis are known only from the late Arikareean of Oregon, M. elatns from the late Arikareean/early Hemingfordian of Nebraska, and $M$. hollandi from the early Hemingfordian of Nebraska and Wyoming. Contemporary materials from other areas are few and for the most part too fragmentary for taxonomic treatment. Scattered remains from Oregon to Florida do suggest a broad geographic range and probably a more complex early Miocene evolutionary story than can currently be reconstructed. Moropas is mlich more common in the fluvial channel fills in the base of the Upper Harrison Formation than in any other rock unit (Hunt, personal communication). This high rate of occurrence of Moropns elatus in particular could be a result of its relatively greater abundance or could be related to dietary, herding, or other habits that made them more liable to preservation. On the other hand, the conditions of deposition of the Upper Harrison Formation could have been unusually conducive to chalicothere entombment.

The earliest documented occurrences of Moropus in North America are late Arikareean. At this time or somewhat earlier the genus apparently immigrated from Eurasia across the Bering land bridge or migrated southward as part of a hitherto unsampled northern Holarctic fauna. An Eurasian origin is supported by the absence of chalicotheres in North American Oligocene deposits and their presence in the Oligocene of Eurasia (Oreinotherium bilobatum from the Oligocene of Saskatchewan is a brontothere, not a chalicothere, as Skinner. 1968, also asserted), the presence of small Moropus sp. very similar to M. elatus in the European Aquitanian (Coombs, 1974), and the late Arikareean or early

Hemingfordian appearance in North America of other immigrants from Eurasia (see, for example, the amphicyonids Cynelos and Ysengrinia in Hunt, 1972, and the primitive deer Blastomeryx cited along with other genera by Wilson, 1967, 1968). Floral geography may also be correlated with the early Miocene appearance of Moropus in North America. Wolfe (1969b:85; 1972:230) suggested that the probably early Miocene Collawash flora from Oregon indicated that floristically the warm temperate vegetation at middle latitudes represented a Mixed Mesophytic forest for the first time. At that time the temperate, moist forests of both Oregon
and Alaska contained a number of common species and are considered part of the same floristic province (Wolfe, 1969a:91). Wolfe and Leopold (1967:195) also noted that early Miocene floras of Alaska contained a remarkable number of elements in common with both Oregon and Japan. It is very difficult to associate Moropus with any particular floral element, but its known North American late Arikareean distribution is quite similar to that of the tayassuid Cynorca sociale, whose range was correlated with floral information by Woodburne (1969).

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[^0]:    AM-Pratt Museum, Amherst College, Amherst;
    AMNH-Department of Vertebrate Paleontology, American Museum of Natural History, New York;
    CM—Carnegie Museum of Natural History, Pittsburgh;
    F:AM—Frick American Mammals, American Museum of Natural History, New York;
    FMNH—Field Museum of Natural History, Chicago;
    UCMP—University of California, Museum of Paleontology, Berkeley;
    YPM-Peabody Museum of Natural History, Yale University, New Haven.

    Other abbreviations used are Mc and Mt followed by a Roman numeral to indicate, respectively, metacarpal and metatarsal.

    The anatomical terms generally follow usage by Butler (1965), except where an element was not discussed by him; the terminology utilized by Holland and Peterson (1914) is often obsolete. Directional terminology applied to the skeleton is as follows:

